

STUDIES
ON SCHOENUS VEGETATION
IN SOUTH AND SOUTHEAST
SWEDEN

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SWEDEN

- I. Classification of Schoenus communities in South and Southeast Sweden
- II. Schoenus vegetation and environmental conditions in South and Southeast Sweden.
- III. Soil acidity and distribution of species on tussocks and interspaces in Schoenus vegetation of South and Southeast Sweden.

by

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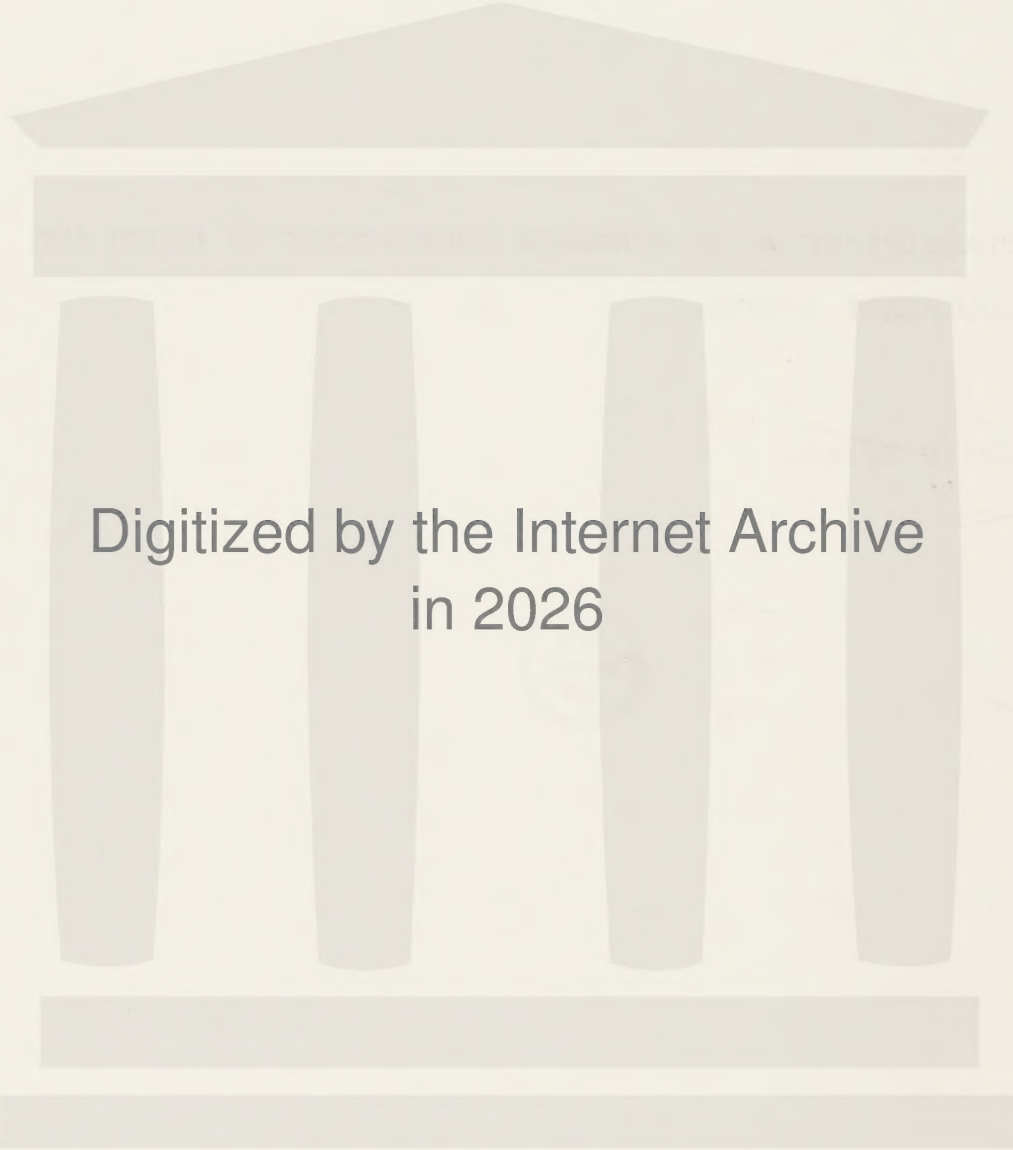
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Diversity, Homotoneity, Oxycoccus-Schoenus ferrugineus association, Primula-Schoenus ferrugineus association, Schoenus nigricans phytocoenon, Succession, TABORD-classification.

Nomenclature follows Lid (1974) for vascular plants, Nyholm (1954-196) for Musci, Müller (1951-1957) for Hepaticae. Bryum pseudotriquetrum includes B. bimum, and Mnium seligeri M. affine. Schoenus-tussocks with leaves and bracts intermediate in length and undeveloped spikelets are here called S. intermedius. The taxonomy of the genus is however unexplored (Görs 1964:9, Kloss 1965:77, Braun 1968:60) and often S. nigricans seems to be of the intermedius type.

Syntaxon names are adopted from Oberdorfer (1957), Westhoff & Den Held (1969) and Braun (1970).

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Introduction

Schoenus phytocoenoses (concrete individual stands of vegetation according to Westhoff & van der Maarel 1973) occur on sites with a high water table, at least in winter and spring. I prefer to call such sites wetlands (cf Sjörs 1971) instead of more specifically fen (minerotrophic mire, i.e. ecosystem or even area with peat formation, Sjörs op.cit.) because Schoenus sites do not always contain peat (highly organic material accumulated under anaerobic conditions, compare e.g., Stålfelt 1969). This paper concerns the geographical variation of the Schoenus dominated phytocoena (abstract, unclassified community according to Westhoff & van der Maarel 1973), to be distinguished in S and SE Sweden. The ecological relationships of these types will be treated in a subsequent paper (Tyler 1979a). Schoenus wetlands were chosen as an object of the study because (i) they are rather rare and valuable, but threatened communities in Sweden, (ii) they are comparatively easy to delimit from other wetland communities, and (iii) they can be very well studied in a wider European context.

Swedish mire research has paid little attention for a long time to the vegetation of mires in districts with calcareous soils. Complete vegetation analyses of South Swedish Schoenus phytocoenoses, (i.e., including all layers and with quantitative data on occurrences) except from Öland and Östergötland, were published by Waldheim & Weimarck (1943) and Waldheim (1949) from Skåne (Scania), by Albertson (1942), Albertson & Larsson (1960) and Larsson (1967) from Västergötland, by Almquist (1929) from Uppland and Gästrikland, and by Ljungquist (1929) and Pettersson (1958) from Gotland. In total 107 relevés from 35 wetlands are available from these sources.

The original Swedish mire terminology, most of it defined by Du Rietz (1949, 1954, 1961 i.a.) has gradually been modified, e.g., by Sjörs (1948), who distinguished three vegetation

gradients: (i) 'poor - rich' , (ii) 'hummocks - lower hummocks-lawns (+tussocky) - carpets - mudbottoms', and (iii) 'mire margins - mire expanses'. The Schoenus phytocoenoses have long been regarded as belonging to 'rich fens' or even 'extremely rich fens' (Waldheim & Weimarck, op.cit.) and, according to Sjörs (1948, 1950), to 'a lawn community of the mire expanse'. In Sweden, a few large-scale attempts have been undertaken to obtain synoptic tables from a larger region or a certain group of phytocoena (Tyler, 1969b).

The ability of Schoenus to build up tussocks is prerequisite for the settlement of both wet-growing species like several bryophytes and drier-growing like Potentilla erecta. Tussocks and interspaces, each with their typical species compositions, depend on each other and the combination is both natural and stable. In continental Europe the 'Schoenetum' always includes both the phytocoenoses on and those between the tussocks (e.g., Görs 1964). In Sweden, Larsson (1967) considers it to be a vegetation complex and analyzes the components separately, but most other authors handle the Schoenus phytocoenosis as a unit, though with some hesitation.

Materials and methods

Field investigations

The investigated wetlands are located in five South Swedish provinces (Fig. 1), all regions with superficial deposits rich in lime although the calcium carbonate content of the substrate is often low. The average temperature of July is c.17°C and the mean precipitation is 400-500 mm per year on Öland and Gotland, otherwise 500-600 mm (SMHI 1977). Skåne has more than one month longer vegetational period (number of days with mean temperature >3°C) than Uppland. During that period Öland and Gotland have an arid climate and the other provinces a subarid (Atlas över Sverige 1953). In each province I have chosen 10-13 wetland areas where Schoenus is known to occur according to the literature and personal communications.

The areas have been distributed as uniformly as possible in each region, and in such a way that all types of wetlands with Schoenus are represented. In Skåne, where Schoenus is particularly rare, all Schoenus stands (phytocoenoses) have been investigated. In larger wetlands, where the Schoenus stands are separated by other vegetation, the stands are treated as separate units. Stands of Schoenus nigricans or S. intermedius have always been separated from stands of S. ferrugineus. A short description of every site and its geographical position is given in Tyler (1979b).

Field work was carried out in the summers of 1972 and 1973. In each site three relevés were made, i.e., squares of 4 m². The size was chosen after determination of the minimal area (Ellenberg 1956) in Scanian phytocoenoses (cf. also Kovács 1962:16). The species composition of the whole stand as well as of contact vegetation was always recorded. Very small stands were either analyzed by only one standard area or treated as a unit. The squares were located at random but distinctly heterogeneous vegetation was avoided. The cover of each species was estimated according to the scale of Hult-Sernander-Du Rietz (sensu Trass & Malmer 1974) with an additional scale value for cover $< \frac{1}{400}$.

Numerical methods

The relevés were arranged into phytocoena using the TABORD program (van der Maarel, Janssen & Louppen 1978, see also Bouxin 1975, Persson 1977). The extended Hult-Sernander-Du Rietz scale has been rescaled from 1 to 6 before calculating the similarity ratios. The TABORD program was applied with various options, both to the whole data set and to parts thereof. These options are indicated as TABORD 30, TABORD 40, TABORD 60a and TABORD 60b with threshold and fusion levels 0.30/0.50, 0.40/0.60, 0.60/0.80, and 0.60/0.85 respectively.

Spectra for life forms and morphological forms were calculated for each phytocoenon according to Ellenberg (1974) using the product of presence and characteristic degree of cover (Malmer 1962) as quantitative value per species per synoptic table. Similarly a syntaxonomical spectrum was calculated.

In order to compare and characterize different phytocoena their homotoneity was studied (Dahl 1957, 1960, Moravec 1971, 1973, and Westhoff & van der Maarel 1973). The relevés of a cluster are considered to constitute a homotoneous phytocoenon if the ratio of the Raunkiaer presence classes IV + V to II + III is slightly over 1, the ratio of classes III + IV + V to II is about 2 and the ratio of classes V and IV 1 (Westhoff & van der Maarel, op. cit.:647). The diversity index, α , was calculated according to Dahl (1960:807). The index of uniformity, S_A/α , was determined from Fig. 1 in Dahl (loc.cit.), as obtained from the relationship between S_N/S_A and N , and then the correct value of α was calculated. N is the number of relevés, S_N the total number of species in N relevés, and S_A the mean number of species per relevé. If the index of uniformity is high, 1.2 in phytocoena poor in species, 'all the usual criteria can be expected to give indications of high homotoneity' (Dahl 1957:59). The basic homotoneity index according to Moravec (1971), bH^I , was calculated as

$$\frac{\sum_{i=1}^p C_i (V+IV)}{S_A} \quad (1)$$

where C is the mean percentage presence of the given presence classes of N relevés and species i — p . For $N > 20$ the approximations given by Moravec (1973) were used, for $5 < N \leq 20$ the tables given by Češka (1966). With $N < 5$ the proposals by Moravec (1973) were followed.

Westhoff & van der Maarel present the formula

$$\frac{\sum_{i=1}^p C_i (V+IV)}{S_N} \quad (2)$$

which has also been used.

Finally the homotoneity was estimated as the average within-cluster similarity as calculated in the TABORD procedure using the formula:

$$S_{x,z} = \frac{N \sum x_i z_i}{N^2 \sum x_i^2 + \sum z_i^2 - N \sum x_i z_i} \quad (i=1, \dots, n) \quad (3)$$

for the similarity between one single relevé x and cluster z and averaging this value over the relevés of z .

In (3) x_i is the score of species i in relevé x , z_i is the sum of scores of species i in the relevés of cluster z , N is the number of relevés in cluster z and n the number of species occurring in either relevé or cluster (van der Maarel et al. 1978).

Arrangement of synoptic table

The clusters given by TABORD were arranged according to similar patterns in species composition. Species with similar distribution as to environmental conditions were grouped together. I also tried to derive syntaxonomical species groups on the basis of own material, as well as Waldheim 1943, and unpubl., Oberdorfer 1957, Malmer 1962, Braun 1968, 1970, Klötzli 1969, Mörnsjö 1969, Westhoff & Den Held 1969, Tyler 1969, Andersson 1970, Hallberg 1971, Larsson 1974, 1976, Regnéll 1974, 1975, 1976, and the papers mentioned in the introduction.

Both the species groups and the syntaxonomical classification are tentative, due to lack of reference tables and a working syntaxonomy from Fennoscandia.

Classification

TABORD-groupings

The whole material consists of 189 relevés and 289 species. All relevés and the 200 most frequent species were included in the data matrix. At the TABORD 40 level the relevés were grouped in six clusters (Fig. 2) and a remainder of ten relevés. The position of five relevés of the remainder was determined in a separate run and a cluster 7 was formed (for further details see Tyler 1979b). At the TABORD 30 level the clusters 6 and 7 were combined, though their only common species is Schoenus nigricans. Clusters 1-4 and 6 have 14-16 constant species (constancy level 60 per cent presence), cluster 5 only five and cluster 7 only three constant species. The Schoenus ferrugineus clusters (1-4) show a low similarity to the Schoenus nigricans clusters (5-7) (Tyler, op.cit.).

The large cluster 1 was treated separately on the TABORD 60a and b levels (124 relevés, 124 species) and seven new clusters were formed. Several of them are very similar (>0.70) and none less than 0.40 (Tyler, op.cit.). Except for cluster 16 all clusters have more than 20 constant species. Cluster 4 (35 relevés, 84 species) was divided into five parts when separately treated on the TABORD 60a level. Most of the new clusters have similarity ratios of <0.70 and some of <0.40 . The number of constant species varies but is mostly 14-20. Species with very high cover play a great rôle for the similarity ratios in TABORD, e.g., the high cover of Calliergonella results in formation of cluster 13-14. Remainder relevés were included in every new run and all but ten were placed in clusters at any level. Also higher homotoneity levels (threshold values) were used and cluster 13 and 15-17 were all split up (Tyler, op.cit.).

Syntaxonomical rank of clusters

It seems justified to regard clusters of TABORD 40 (1-6) as associations (cf Westhoff & van der Maarel 1973, Kortekaas et al. 1976). However, the clusters 2, 3, 5, 6 and 7 consist of too few relevés and may only be considered as potential nuclei for associations. Clusters on the next homogeneity level (0.60) may be regarded as subassociations, but I prefer to regard them, as well as the nuclei, as unclassified phytocoena. Only clusters 1 and 4 are given syntaxonomical names, and the nucleus 2 is added to cluster 1 forming an association *sensu lato* (Fig. 2).

Species groups

The differential species of Table 2 (species group A) have often very low presence and some of them are not restricted to one or two phytocoena. Their information values seem to be low. Nevertheless, I have found it practical to place them here. The distribution of several species is geographically limited. Selaginella selaginoides and Drepanocladus badius are northern species with few occurrences in southern Sweden. Cinclidium stygium is also a northern species though less rare in southern Sweden. Oxycoccus quadripetalus, Carex limosa and Drosera anglica are common in the whole investigation area, but in the Schoenus phytocoena mainly restricted to Uppland. Parnassia palustris, Primula farinosa and Preissia quadrata have wide distributions in Sweden - Primula southeastern to Dalarna, Parnassia and Preissia throughout the whole country but more common to the north (Arnell 1956, Hultén 1971). The species Euphrasia salisburgensis to Calamagrostis varia in Table 2 occur only on Gotland. In south Sweden, Bartsia alpina occurs only in Östergötland and Gotland. Pinguicula alpina and Euphrasia salisburgensis are proposed to be late-glacial relicts on Gotland (Sjörs 1956). E. salisburgensis is nowadays parasiting only on Schoenus (Pettersson 1958). Valeriana dioica occurs only in Skåne and Öland.

Several species occur in almost every relevé in this investigation. They are called general species (group B).

The following species groups often include taxa confined to certain phytocoena and may be regarded as characteristic species compositions. Acidophilous or indifferent fen species (group C) play a rôle in the phytocoena of Uppland and Östergötland. The alliance Scorpidio-Utricularion is usually represented in interspaces and larger hollows (puddles) with a high water table (group D). It occurs both in spring fens and in other wet fens mainly in Uppland (mud bottoms, carpets according to Sjörs 1948). Scorpidium scorpidioides often forms large carpets on Gotland on flat ground, submerged only in winter and spring. Phragmites communis is the most common swamp species in the group E, which is of less importance in most phytocoena. Some species of the order Tofieldietalia have an uneven distribution in the phytocoena and mostly low presence. They are gathered in group F. Sometimes the Schoenus wetlands are rather dry, at least in summer, and then characterized by the species of group G. The subassociation groups 'brizetosum' of Braun (1968) and the Stachys officinalis- and Festuca rubra-groups of Klötzli (1969) consist chiefly of the same species. Typical sloping spring fens occur in the whole investigation area but in Skåne and Östergötland most Schoenus sites are nowadays cultivated. The spring fens, being of less agricultural value, remain and so this type is the most frequent in these provinces. The species in group H are chiefly the same as those given by Braun (1970) as character species of Cratoneurion. The group I, wet-meadow species, consists of species belonging mostly to Moliniétalia and perhaps indicating a more fluctuating water table and less nutrient-poor conditions than usual in Schoenus phytocoenoses (Braun 1968:91, 94-95, Klötzli 1969:74-75, 80). According to Arnell (1956) the only species of group J, Riccardia sinuata, grows on very wet peat, that is mostly in the interspaces. This behavior contradicts the experience of the present author. The

species is of importance in a few phytocoena, mainly those of Skåne. The 'acid peat species', group K, grow on the top of the very high tussocks of Schoenus (mostly nigricans) in Skåne. ('Peat' is in this case used in a broad sense, meaning highly organic material, regardless of aerobic conditions as, e.g., 'Anmoor' sensu Göttlich 1956). The pH of the top 'peat' is about 5.0 compared to 6.8 in the muddy interspaces (mean of 12 measurements made directly in the 'peat'). For similar findings see van der Maarel & Leertouwer 1967 . Shrubs and trees are gathered in group L.

Phytocoena

The associations of Oxycoccus-Schoenus ferrugineus and Primula-Schoenus ferrugineus are well separated by their differential species (Table 2), and their main distribution areas are different (Fig. 1). One phytocoenon in each association may be regarded as transitional types, namely the Sesleria-Carex hostiana and the Myrica phytocoena.

The Oxycoccus-Schoenus ferrugineus association is divided in four phytocoena, of which two occur on each Öland and Gotland. The four phytocoena are distinguished by several species (Table 2). The Primula-Schoenus ferrugineus association is divided into three regionally delimited groups, i.e., the Sesleria , Bartsia-Ophrys , and Valeriana groups (Figs. 1 and 2). The groups, as well as their subdivisions, are well separated by differential species (Table 2), but Ophrys insectifera and Bartsia alpina are very weak differential species of the Bartsia-Ophrys group. All nuclei but the Cladium-Schoenus nigricans phytocoenon have several species in common with the Primula-Schoenus ferrugineus association though they are distinguished by the presence of Schoenus nigricans, Schoenus intermedius, seashore species or liverworts. The presence of several species separate the Cladium-Schoenus nigricans phytocoenon

from all other investigated phytocoena (Table 2).

Life forms, morphological forms and syntaxa

Most clusters are dominated by hemicryptophytes, which, together with geophytes, make up more than 80 per cent of the sum of the importance values (Table 2). Only in clusters 41-44 do other life forms constitute the main part (hydrophytes, geophytes, nanophanerophytes, and dwarf shrubs). Therophytes play a very modest part in most clusters, except in clusters 2, 3, and 7, where they constitute 6-11 per cent. The winter aspect is greener in phytocoenoses belonging to clusters 41-44 and 7 than in all others. Helomorphic, mesomorphic and scleromorphic plants together dominate all clusters though in slightly different proportions. Hydro-morphic plants and succulents play a rôle only in clusters 42-44 and 7.

Only in clusters 43, 44 and 7 do syntaxonomical groups other than those of Scheuchzerio-Caricetea, Tofieldietalia and Eriophorion latifolii constitute more than 50 per cent of all syntaxa. Asteretalia + Plantaginietalia make up 35 per cent in cluster 7 and several syntaxa are mixed in clusters 43 and 44, e.g., Sphagno-Utricularion and Rhynchosporion. Species of the classes Molinio-Arrhenateretea and Phragmitetea and their subdivisions are frequent in clusters 12-18, 3 and 6, but they never play a dominating rôle.

According to Ellenberg (1974) all distinguished phytocoena, except the Utricularia subunits of the Oxycoccus-Schoenus ferrugineus association (clusters 43, 44), ought to be regarded as belonging to Eriophorion latifolii (= Caricion davallianae, Westhoff & Den Held 1969), although with a certain admixture of other syntaxa. The two odd Utricularia phytocoena of the Oxycoccus-Schoenus ferrugineus association are mixtures of several syntaxa but perhaps most associated with Scheuchzerio-Caricetalia.

Homotoneity and diversity

There has always been a strict demand for homogeneity of studied vegetation. When the relevés are combined to phytocoena there is also a need for evaluation of the results in respect to homotoneity (term first used by Nordhagen 1943). Seven different indices are used in the present study and their similarity in measuring the homotoneity will be discussed.

The average coefficient, calculated by TABORD, is a measure of to which extent the relevés of a cluster are gathered near the centroid, within the limits given by the homotoneity level (= threshold value). Average coefficients on different levels cannot be compared. The similarity in presence and cover of the species is calculated. All other indices use the presence degrees of species only.

The index of diversity is, in a way, a measure of how long the 'species tail' of a table is, i.e., the difference between the relevés in number of species. A high index of diversity may be the result of i) heterogeneity of sample areas, ii) too small sample areas, iii) too few relevés, iv) a phytocoenon rich in species, many with low presence, v) a heterotoneous cluster. These causes are not independent of each other, ii, iii and iv may be related. The index of uniformity is a measure of how much of the 'tail' is considered in the mean number of species. Highly similar phytocoena have about the same values of these two indices. If, however, some of these phytocoenoses are not in equilibrium with the environmental conditions, i.e., are being invaded by new species, the 'species tail' grows, at least in the beginning of the changes, giving new values of the indices. So these indices may be used as measures of the degree of equilibrium provided the values of the equilibrium state can be estimated. However, Dahl (1957) demonstrates that if the uniformity index is below 1.2, presence class V will be smaller than IV. Nevertheless, the phytocoenon

may still be homotoneous, especially if the number of species is high. In such a case the index fails to measure the homotoneity. In the present study many phytocoena must be considered as rich in species, at least for Scandinavian conditions.

The two indices of Raunkiaer calculate to what extent the species with high presence dominate in the table. The indices of basic homotoneity also calculate the dominance of these species, but as a mean of several means. The difference between bH^I and bH^{II} is that the first mentioned is a standardized value. The values of these indices vary independently. bH^{II} is more dependent on rank of the phytocoenon and is more sensitive. It must be considered as more correct. I have not found any reference to comparisons of these indices, so I propose an arbitrary limit of 40 for bH^I and 15 for bH^{II} for minimum homotoneity values, after having compared my own values with values estimated from the associations and subassociations of Hallberg (1971).

The average coefficients on the TABORD 40 level vary between 0.54 and 0.72 (Table 1). Almost all clusters on the TABORD 60 levels have coefficients above 0.70. The index of diversity varies between 17 and 38. Clusters 13-15, 4, 13+14, and 16+17 have the highest diversity. The values of the ratios V/IV and S_A/α sometimes diverge. Many clusters have either too low values of both ratios or of one of them. The values of the other ratios of Raunkiaer are in most cases acceptable or high, when the two ratios, V/IV and S_A/α are sufficiently high, but sometimes they do not tally. Only two clusters have bH^I values below 40, clusters 7 and 5. These two clusters, in addition to clusters 4, 13+14, 16+17 and 16, also have values below 15 of the bH^{II} . No less than six of the clusters have $bH^I > 60$. None of the indices used show perfect covariation of the values; on the contrary most values vary independently. The covariation is rather good only between bH^{II} and the diversity and uniformity

indices. High average coefficients do not always imply homotoneity as measured with bH^{II} .

The agreement between the different indices is low, due to the fact that they give different measures of homotoneity. Therefore they can be used in combinations in order to describe different properties of the species composition of a phytocoenon, e.g., cluster 12 (cf. Table 1). This cluster has a small variability within the TABORD 60 level, a fairly low diversity and a good uniformity. It has a large share of species with a high presence in relation to both the total number and the mean number of species per relevé. The cluster is homotoneous in all respects compared with cluster 13, the values of which are varying. The high diversity and the low homotoneity indicate unstable conditions compared with cluster 12, i.e., the Carex lepidocarpa phytocoenon seems to be more stable than the Calliergonella phytocoenon within the Valeriana group, a fact also discussed below. However, the corresponding phytocoena of the Bartsia-Ophrys group (14 and 15) are quite similar in respect to diversity and homotoneity. The suggested prediction value of the diversity and uniformity indices seems to be uncertain (cf. Whittaker 1972). On the other hand, a very low diversity indicates an early stage in the succession (Whittaker 1975), exemplified by the Utricularia-Drepanocladus phytocoenon (43), compared with the Selaginella-Pinus phytocoenon (41).

Less than half of the clusters are homotoneous as measured by most indices used, but more than half as measured by the two basic homotoneity indices only. Clusters 5 and 7 do not constitute good phytocoena and cannot be divided into more homotoneous clusters, as can 13, 15, 16 and 17 (Tyler 1979b).

Variation in space

The different phytocoena vary in richness in species, in most important species groups, in life forms and morphological forms, and in contact phytocoena. It seems quite clear that most phytocoena of the Primula-Schoenus ferrugineus association are much richer in species than those of the Oxycoccus-Schoenus ferrugineus association, though it is difficult to evaluate the total number of species because the number of relevés is different (Table 2). Within both associations rather high as well as very high means are represented.

Divergence in most important species groups indicates differences in environmental conditions further discussed by Tyler (1979a). Three gradients may be distinguished; i) from inland species to seashore species, ii) from acidophilous to basiphilous species, and iii) from spring-fen and puddle species over swamp and wet-meadow species to drier-meadow species. The first gradient is illustrated by the Glaux and Schoenus intermedius phytocoena, the second by the two associations, as well as by the phytocoena within the Primula-Schoenus ferrugineus association, and the third gradient by phytocoena of both associations (Table 2, 3).

Distinct gradients are obvious in life forms and morphological forms (Table 2). Only in the Oxycoccus-Schoenus ferrugineus phytocoena of Uppland do life forms other than hemicryptophytes and geophytes play an important rôle. Dwarf shrubs may indicate a less favorable climate, but they are sheltered by snow in winter. These conditions are further indicated by the northwards increasing importance of overwintering green plants. In all phytocoena helomorphic (marsh) plants are wholly dominating, but some phytocoena occur in drier conditions, e.g., the Sesleria group and the Calliergonella phytocoenon of the Bartsia-Ophrys group.

Dissimilarities in contact phytocoena is connected with the dissimilarities in species groups and zonations are common (Table 3). Sesleria meadows, where Sesleria coerulea and Molinia coerulea are dominating species and Carex flacca, Carex hostiana, Briza media, Primula farinosa, Centaurea jacea, Inula salicina, Juniperus communis, and Ctenidium molluscum i.a. are accompanying species, often surround Schoenus wetlands with Tofieldia or Carex hostiana phytocoenoses (Fig. 3A). The Sesleria meadows of Upland are slightly different with occurrence of Carex nigra, Carex panicea, and Filipendula ulmaria. In Carex flacca- and Molinia coerulea-dominated meadows, bordering on Schoenus wetlands with Calliergonella phytocoenoses of the Bartsia-Ophrys group, Crepis paludosa, Equisetum palustre, Epipactis palustris, Calliergonella cuspidata, and Mnium seligeri are common species. The Molinia meadows, adjacent to Schoenus wetlands with Calliergonella phytocoenoses of the Valeriana group, differ in that Valeriana dioica, Sieglingia decumbens, Festuca ovina and Campylium stellatum are important species (cf. Tyler 1975, Regn  ll 1976).

Distinct zonations occur from the sea up to the Sesleria meadow (Fig. 3B). In the few sites investigated on Gotland, Scirpus tabernaemontani reeds are followed by Glaux-Schoenus nigricans, Schoenus intermedius-Schoenus ferrugineus, and Tofieldia-Schoenus ferrugineus wetlands, and Sesleria meadows, in the sequence mentioned. On   land, no Schoenus nigricans or Schoenus intermedius zone has been investigated. Glaux-Schoenus ferrugineus phytocoenoses are developed here between Scirpus rufus-Scirpus quinqueflorus and Carex hostiana phytocoenoses. On the shores of the recurrent Chara pools Carex panicea, Carex nigra, Carex pulchella, Carex hostiana, Scirpus uniglumis and Triglochin palustre grow closest to the water table, and these phytocoenoses sometimes are bordering on Schoenus wetlands with Carex hostiana phytocoenoses (Fig. 3B). Cladium swamps are not uncommon on Gotland,   land and in Upland, and their species composition

is fairly uniform with, e.g., Lythrum salicaria, Mentha aquatica, Pedicularis palustris, Galium palustre, Hydrocotyle vulgare, and, sometimes, Myrica gale. The zonation Cladium — Schoenus nigricans — Schoenus ferrugineus phytocoenoses described by, e.g., Zobrist (1935), is not often met with in Sweden, where it is represented by the zonation Cladium — Cladium-Schoenus nigricans — Schoenus intermedius-Schoenus ferrugineus (sometimes) — Tofieldia phytocoenoses (Table 3, Fig. 3B). The Cladium swamps may also be bordering on Schoenus wetlands, where Myrica gale and Oxycoccus quadripetalus are important species. In Uppland, some sites have been investigated, where a pool is surrounded by a quagmire, overgrown by Scorpidium scorpidioides and Drepanocladus species. In the quagmire, a zone with Schoenus ferrugineus phytocoenoses of the Utricularia-Drepanocladus type occurs. This zone is followed by Selaginella-Pinus phytocoenoses (Oxycoccus-Schoenus ferrugineus ass.), Myrica-Pinus phytocoenoses and finally a Ledum-Pinus bog of common East Swedish type (cf Malmer 1965:151). Sometimes the pool and quagmire are replaced by a Carex lasiocarpa-Phragmites communis or a Carex buxbaumii fen (Table 3, Fig. 3B). In sloping spring fens the flushing water is captured by bryophyte phytocoenoses (Cratoneurum commutatum-dominated) and the Schoenus ferrugineus phytocoenosis is developed between these and other contact phytocoenoses dominated by, e.g., Juncus subnodulosus and with occurrences of Valeriana dioica, Filipendula ulmaria, Cirsium palustre, and Calliergonella cuspidata (Fig. 3C, D).

Variation in time

A combined study of species groups, contact phytocoenoses and earlier investigations of Schoenus phytocoenoses, similar in character, makes it possible to follow the development and to anticipate their faith in the future provided the changes of the environmental conditions proceed in same directions as during the last two to five decades (Table 3).

In Uppland Almquist (1929) distinguished three Schoenus phytocoena:

- 'Schoenus ferrugineus-Amblystegia fens' --
(moist)
- 'Myrica-Schoenus ferrugineus fens' --
(wet)
- 'Carex lasiocarpa-Schoenus ferrugineus fens'
(very wet)

and, as a variant of ordinary 'Ledum-Pinus woodlands (bogs)', 'Pinus-Ledum (Calluna) -Schoenus ferrugineus woodlands'. (Amblystegia = Campyllum, Drepanocladus and Scorpidium species). However, species composition was given only for the Schoenus ferrugineus-Amblystegia fens, which were stated as the typical Schoenus ferrugineus phytocoenon. Myrica gale, Oxycoccus quadripetalus, Andromeda polifolia, Selaginella selaginoides, Phragmites communis, Scorpidium scorpidiodes, Riccardia pinguis, Molinia coerulea and Carex panicea played a less important rôle in these Schoenus ferrugineus-Amblystegia fens than in the Selaginella-Pinus phytocoenon of today. Pinus and Betula were completely lacking. It seems reasonable to assume that this typical phytocoenon has become very rare in Uppland and is nowadays replaced by the Selaginella-Pinus phytocoenon. The investigated wetlands are partly the same in both studies. Physiognomically the Selaginella-Pinus phytocoenosis resembles a Ledum-Pinus bog with Myrica gale instead of Ledum palustre and with sparse Phragmites communis. The field- and bottom-layers are, however, different. The zonation, mentioned above, and the observations of Almquist (op.cit.), indicate the probable succession: Utricularia-Drepanocladus -- Selaginella-Pinus -- Ledum-Pinus, the last stage without Schoenus. Since Myrica gale occurs in several Schoenus phytocoena but Oxycoccus quadripetalus is a good differential species from the Primula-Schoenus ferrugineus association, I prefer the name Oxycoccus-Schoenus ferrugineus association, instead of Myrica-Schoenus ferrugineus used by Ljungquist (1927 1929), Almquist (op.cit.), and Pettersson (1958).

One of the first Swedish studies on calcareous wetlands was made by Ljungquist in 1919-1929. He described a large, nowadays destroyed, wetland area with a Schoenus ferrugineus phytocoenon very similar to one of the subunits of the Tofieldia phytocoenon (Tyler 1979b), and a Cladium-Schoenus nigricans phytocoenon quite similar to my Cladium-Schoenus nigricans phytocoenon. The few relevés of Pettersson (1958) are not distinctly different from the last mentioned phytocoenon either. These relevés were considered most closely related to the Magnocaricion syntaxa. Comparisons of the present Tofieldia phytocoenon with the species compositions and the observations presented by Pettersson (op.cit.) show, that the Schoenus sites, formerly grazed but nowadays mainly ungrazed, seem to have developed towards Sesleria meadows. Pettersson observed that when grazing ceases the number of species decreases and a rapid succession towards meadow conditions occurs. Campylium stellatum and Ctenidium molluscum attain dominance because the site is no longer damaged by trampling.

Du Rietz (1961) presented a small-square analysis of the shrub- and field-layers at Freberga, Östergötland (site 43, Tyler 1979b) made in 1938. It is not certain that his and my relevés are from the same stand (several small ones occurred in 1972) but, if they are, the differences between them are striking in that the species composition is the same but frequency and cover different. The succession is clearly towards a Molinia meadow and perhaps a woodland, that is the same development as for most other phytocoenoses of the Calliergonella phytocoenon (no. 15). The presence of spruce makes the physiognomy of the Calliergonella phytocoenoses quite different from all other Schoenus phytocoenoses in southern Sweden. The tree- or shrublayer is often a mixture of spruce, birch and pine, the last-mentioned species less frequent, however. The conifers are often rather small on the mire expanse and have a slender appearance. The closure of the canopy is mostly low.

Waldheim & Weimarck (1943) and Waldheim (1949) have described the phytocoenoses at Rinnebäck and Örup, Skåne (site nos. 2 and 8, Tyler 1979b). The phytocoenoses of these sites are included in the Calliergonella phytocoenon of the Valeriana group (no. 13). Örup is also described in detail by Tyler (1975), where the changes since 1944 are discussed. The differences at the site Rinnebäck indicates drier and perhaps more nutrient-rich environmental conditions in 1973, a succession towards Molinietum. In fact the site was ditched in 1948 (Waldheim unpubl.) and the situation is even worse in 1978 since the area has been thoroughly grazed by goats (sic!). At the site Örup, the Schoenus ferrugineus phytocoenosis seems to be threaten by a Juncus subnodulosus phytocoenosis.

The Fissidens-Schoenus nigricans phytocoenon (no. 6, including all known Schoenus nigricans occurrences in Skåne) is separated from other Swedish S. nigricans phytocoena in almost all respects. The environmental conditions seem to be quite different. The tussocks are much higher and much more closely spaced in Skåne. These Scanian phytocoenoses were also investigated by Waldheim (1949) at one of the two sites (Örup, no. 8, Tyler 1979). Waldheim combined the Schoenus nigricans and the Schoenus ferrugineus phytocoenoses into one phytocoenon, called Schoenus communities, but today they constitute two phytocoena, very well separated.

The successions of South Swedish Schoenus phytocoenoses may be divided into two types, one natural caused by land upheaval, occurring in Uppland, and a second man-made, or at least accelerated by man. In Uppland, the land upheaval causes drainage and filling-up of the shallow lakes, which develop towards fens. This development is also helped by choking by vegetation. When the peat has lost contact with the calcareous soil water, the final vegetation seems to be a Ledum-Pinus bog. Man-made succession is caused by grazing, which nowadays has ceased, and mostly ditching resulting in fertilization and decalcification. The Schoenus wetlands change to Molinia or

Sesleria meadows and finally probably coniferous or deciduous woodlands (cf. Jensen 1976). Calliergonella cuspidata seems to be a species typical of these Schoenus phytocoenoses in alteration.

Summary

The Schoenus phytocoenoses of south and south-eastern Sweden have been sampled by 189 relevés of standard areas (4 m^2) and divided into clusters using the TABORD program on two homogeneity levels. Two Schoenus associations and five potential nuclei of associations, mainly Schoenus nigricans phytocoena, have been distinguished. The Primula-Schoenus ferrugineus association consists of three groups of phytocoena: the Sesleria, Bartsia-Ophrys, and Valeriana groups with distribution Öland-Gotland, Östergötland and Skåne, respectively. The Oxycoccus-Schoenus ferrugineus association is divided into five phytocoena, three of which occur in Uppland and one each on Gotland and Öland. One Schoenus nigricans phytocoenon occurs in Skåne and the others on Gotland.

The species have been divided into twelve groups in accordance with the similar distribution amongst phytocoena and assumed environmental preferences. Acidophilous or indifferent species together with common mire species are characteristic of the Oxycoccus-Schoenus ferrugineus association, while basiphilous and wet-meadow species are typical of the Primula-Schoenus ferrugineus association and the Fissidens-Schoenus nigricans phytocoenon. Liverworts on 'acid peat' are also typical of the latter phytocoenon. The Glaux phytocoena occur on the seashores of Öland and Gotland and comprise mixtures of fen and seashore species. The Cladium-Schoenus nigricans phytocoenon is part of the zonation Cladium-Schoenus nigricans-Schoenus ferrugineus. The Primula-Schoenus ferrugineus association is characterized by species associated with Tofieldia and Eriophorum latifolium, while in the Oxycoccus-Schoenus

ferrugineus association also Scheuchzerio-Caricetalia and Oxycocco-Sphagnetalia species play an important rôle. Another difference between the two associations is that hemi-cryptophytes and helomorphes dominate in the Primula-Schoenus ferrugineus association, while in the Oxycoccus-Schoenus ferrugineus association dwarf shrubs, hydrophytes and hydro-morphes are rather common.

Based on relevés in literature, changes in the phytocoena of Uppland and in several phytocoenoses of Gotland, Östergötland and Skåne are discussed. Successions towards Ledum-Pinus bogs in Uppland and Molinietum or Seslerietum and finally woodlands in the other provinces are presumed.

The properties of the homotoneity and diversity indices used are compared and their compatibility is discussed. Most clusters are found to be homotoneous when measured with the basic homotoneity indices. High diversity may indicate an early stage in succession (as within the Oxycoccus-Schoenus ferrugineus association) or changes in progress at the time of investigation (within the Primula-Schoenus ferrugineus association).

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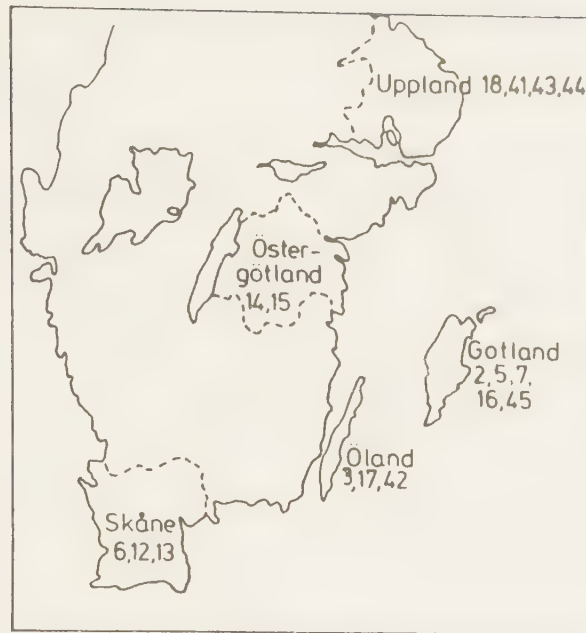


Fig. 1. Map of the investigation area in South Sweden.
Numbers refer to the phytocoena, cf., Fig. 2.

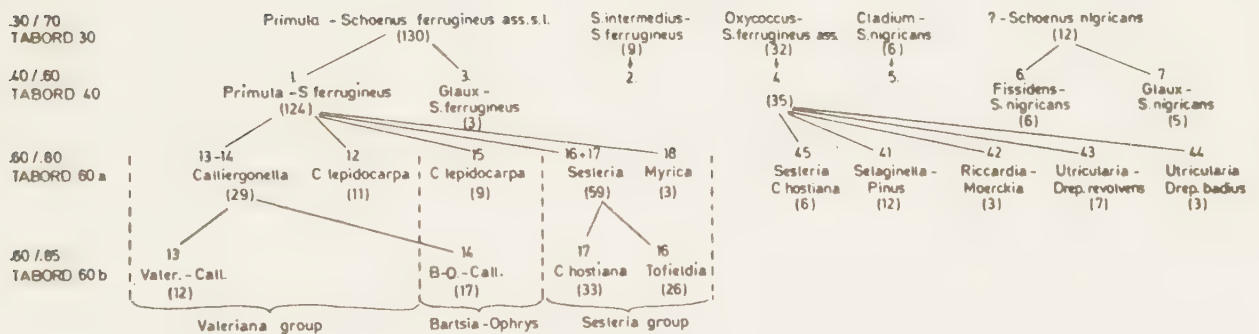


Fig. 2. The TABORD-classification. Threshold and fusion levels are given to the left. The cluster numbers stand above the names of the phytocoena and the number of relevés in each cluster within brackets below the names.

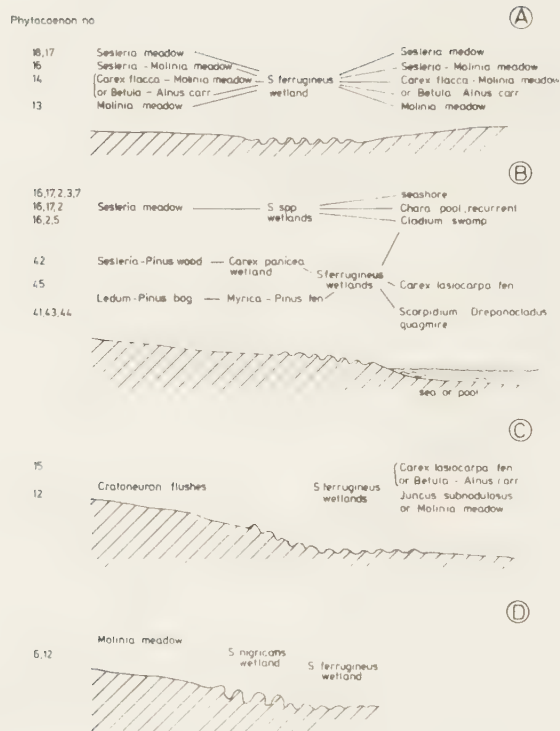


Fig. 3. Contact phytocoena of Schoenus wetlands in Southern weden. A. Schoenus wetlands in shallow depressions. B. Schoenus wetlands above pools or the sea. C. Schoenus wetlands below springs. D. Schoenus nigricans wetlands in Scania.

Cluster no.	Number of relvés	Average coefficient	Raunkjaer's index			Uniformity index	Basic homotoneity index		Diversity index
			$\frac{V+IV}{II+III}$	$\frac{V+IV+III}{II}$	$\frac{V}{IV}$		bH ^I	bH ^{II}	
12	12	.74	1.9	3.0	1.4	1.9	74	36	17.9
13+14	29	.71	.7	1.5	1.4	1.0	44	11	36.0
13	12	.70	.8	2.0	2.0	1.2	47	17	31.7
14	16	.72	1.0	4.9	3.0	1.0	51	15	34.0
15	9	.66	.6	1.2	1.2	1.0	52	18	36.0
16+17	59	.72	.9	3.1	1.3	.8	49	9	33.8
16	26	.75	.5	1.0	3.7	1.0	51	13	28.4
17	33	.73	1.2	2.3	.7	1.0	58	15	27.0
18	3	.70	-	-	-	-	67	45	-
2	9	.64	1.1	2.6	1.1	.8	59	19	26.2
3	3	.54	-	-	-	-	52	28	-
4	32	.63	.7	1.7	.6	.7	44	8	38.5
41	12	.72	.6	1.4	1.8	1.1	52	18	25.4
42	3	.76	-	-	-	-	77	58	-
43	7	.79	1.7	4.4	1.8	2.0	62	34	11.5
44	3	.75	-	-	-	-	73	48	-
45	6	.69	1.7	2.4	4.0	1.4	67	32	17.8
5	6	.72	.4	1.4	4.0	.7	36	13	17.1
6	6	.72	1.3	7.7	2.8	1.3	55	25	17.7
7	5	.59	.4	.9	.4	.8	33	13	24.0

Table 1. Homotoneity and diversity of clusters.

Table 2. Schoenus phytoceon in the SE Sweden.

Cluster no.	Utricularia-Schoenus ferrugineus association					Primula-Schoenus ferrugineus association											
	Utricularia-Drepanocladus badius phytocoenon	Utricularia-Drepanocladus revolvens phytocoenon	Riccardia sinuata-Moerckia phytocoenon	Selaginella-Pinus phytocoenon	Sesleria-Carex hostiana phytocoenon	Cladium-Schoenus nigricans phytocoenon	Glaux-Schoenus nigricans phytocoenon	Glaux-Schoenus ferrugineus phytocoenon	Schoenus intermedius-S. ferrugineus phytocoenon	Bartisia-Schoenus ferrugineus association			Bartisia-Ophrys group		Valeriana group		Fissidens osmundoides-Schoenus nigricans phytocoenon
										Myrica gale phytocoenon	Carex hostiana-phytocoenon	Tofieldia calyculata phytocoenon	Carex lepidocarpa phytocoenon	Calliergonella cuspidata phytocoenon	Calliergonella cuspidata phytocoenon	Carex lepidocarpa phytocoenon	
44	43	42	41	45	5	7	3	2	18	17	16	15	14	13	12	6	
Number of relevés	3	7	3	12	6	4	5	3	9	3	33	26	9	17	12	11	
Total number of species	34	42	39	80	41	33	45	43	62	39	106	104	102	111	104	76	
Mean number of species per relevé	23	23	29	28	19	12	18	23	21	26	27	27	36	34	38	34	
A.																	
T Schoenus ferrugineus	5 ²	V ³	5 ⁵	V ⁴	V ³	.	.	5 ⁴	IV	5 ⁴	V ⁴	V ⁴	V ⁴	V ⁴	V ⁵	V ⁴	.
T Schoenus nigricans						V ³	5 ⁴	.	IV ⁴	.	.	I ²	.	.	.	.	V ⁵
T Schoenus intermedius					II ²	.	.	.	IV ³	.	.	.	.	.	.	.	II
Myrica gale	5 ²	V ²	5	V ²	V ²	.	.	.	IV ³	5 ²	.	I ³	.	.	.	.	.
O Oxycoccus quadripetalus	5	V	4 ²	V	.	.	.	.	.	4	.	.	.	.	.	.	.
T Scirpus hudsonianus	5	IV	4	V	.	.	.	.	.	4	.	.	.	.	.	.	.
S Rhynchospora alba	4	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.
Saccobasis polita	4	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.
Drepanocladus badius	5 ⁴	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
S Carex limosa	4	IV	.	II	.	.	.	.	.	.	.	.	.	.	.	.	.
S Drosera anglica	5	V	4	II	.	.	.	.	.	.	.	I	.	.	.	.	.
P? Carex lasiocarpa	5	V	4	III	.	.	.	.	.	.	.	.	.	.	.	.	.
P? Equisetum fluviatile	.	III	4	II	.	.	.	.	.	.	.	.	.	.	.	.	.
C Cinclidium stygium	.	V	5	V	.	.	.	.	.	4	.	.	III	II	.	.	.
T Selaginella selaginoides	.	.	.	III	.	.	.	.	.	5	.	.	.	.	.	.	.
O Andromeda polifolia	.	.	.	III	.	.	.	.	.	.	.	.	.	.	.	.	.
N Calluna vulgaris	.	.	.	III	.	.	.	.	.	.	.	.	.	.	.	.	.
P Pedicularis palustris	.	.	.	II	.	.	.	.	.	.	.	.	.	.	.	.	.
Ph Cladium mariscus	.	.	.	II	II	II	.	.	.	.	.	.	.	.	.	.	.
M Taraxacum suecicum	.	.	.	II	II	II	.	.	.	.	.	.	.	.	.	.	.
T Juncus alpinus	.	.	.	III	III	III	.	.	.	.	.	.	.	.	.	.	.
T Preissia quadrata	.	.	5	II	.	.	.	.	.	.	IV	II	III	III	IV	V	.
T Primula farinosa	.	.	.	I	II	.	.	5 ²	V	5	V	V	V	V	V	V	.
T Parnassia palustris	.	.	.	V	.	.	.	4	IV	.	III	V	IV	V	IV	IV	.
a Glaux maritima	.	.	.	.	.	.	.	4 ²	.	.	.	.	.	.	.	.	.
ar Leontodon autumnalis	.	.	.	.	.	.	.	4 ²	.	.	.	.	.	.	.	.	.
a Triglochin maritimus	.	.	.	.	.	.	.	3 ²	.	.	.	.	.	.	.	.	.
ar Centaurea littoralis	.	.	.	.	.	.	.	5	.	.	.	I	II	.	.	.	.
ar Tetragonolobus maritimus	.	.	.	.	.	.	.	4 ²	.	.	.	II	I	.	.	.	.
a Plantago maritima	.	.	.	.	.	.	.	2	.	.	.	II	I	.	.	.	.
T? Campyllum polygamum	.	.	.	.	.	.	.	2 ²	5 ²	.	.	.	.	.	.	.	.
ar Potentilla anserina	.	.	.	.	.	.	.	2	4	.	.	.	.	.	.	.	.
ar Juncus maritimus	.	.	.	.	.	.	.	4 ²	.	.	.	.	.	.	.	.	.
T? Sesleria coerules	.	.	.	V ²	.	.	.	.	.	4 ²	V ²	V ²	.	.	.	.	.
T? Carex hostiana	.	.	.	III	III	.	.	.	.	5	IV	I	III	III	.	.	.
T Ophrys insectifera	.	.	.	.	.	.	.	.	.	.	II	I	III	III	.	.	.
T Bartisia alpina	.	.	.	.	.	.	.	.	.	.	.	I	III	III	.	.	.
T Euphrasia salisburgensis	.	.	.	.	.	.	.	.	.	.	.	I	II	I	.	.	.
T Pinquicula alpina	.	.	.	.	.	.	.	.	.	.	.	I	.	.	.	.	.
T Tofieldia calyculata	.	.	.	.	.	.	.	.	.	.	.	II	.	.	.	.	.
T Cymnadenia odoratissima	.	.	.	.	.	.	.	.	.	.	.	III	.	.	.	.	.
T? Calamagrostis varia	.	.	.	.	.	.	.	.	.	.	.	II	.	.	.	.	.
T Carex lepidocarpa	.	.	.	.	.	.	.	.	.	.	.	II	.	.	.	.	.
M Valeriana dioica	.	.	.	.	.	.	.	.	.	.	.	I	IV	.	.	.	.
T Fissidens osmundoides	.	.	.	II	.	.	.	.	.	.	.	.	.	.	III	V	.
B.																	
T Drepanocladus revolvens	.	V ⁴	5 ⁵	V ³	V ²	.	.	.	II	5	V ²	V ²	V ⁴	V ²	V ³	V ⁴	V ²
P Riccardia pinguis	5 ²	V	5	IV	II	II	.	4	.	4	IV	II	V	IV	III	V	II
T Campyllum stellatum	5 ²	V ²	5 ⁴	V ⁴	V ³	V ⁴	.	.	V ⁴	5	V ⁴	V ³	V ³	V ²	V ³	V	II
T Bryum pseudotriquetrum	.	II	5	IV	IV	.	.	.	IV	5	IV	III	V	V	V	V	IV
T Fissidens adiantoides	.	II	5	III ²	V ²	.	.	.	IV	4 ²	IV	V	V	V	V	V	IV
T? Epipactis palustris	.	II	5	IV	.	.	.	.	II	.	II	IV	V	V	V	V	IV
T Pinquicula vulgaris	.	III	.	III	V	.	.	.	II	.	II	IV	V	V	V	.	V
M Carex panicea	.	.	.	.	.	.	.	.	IV	.	IV	II	IV	III	IV	V	.
M? Molinia coerules	.	.	4	V	V	IV	2 ²	.	V	5	IV	IV	IV	III	III ²	4V	.
P? Potentilla erecta	.	.	4	V ²	V ³	V ²	4 ²	.	V ²	5 ³	V ²	V ³	V	V ⁴	V ³	V ³	V ³
T Campyllum elodes	.	.	.	I	V	III	3	.	V	4	V	V	IV	IV	.	.	V
M? Succisa pratensis	.	.	.	.	III	II	3	.	IV	5	IV	IV	IV	V	V	V	.
T Linum catharticum	.	.	.	.	II	.	2	5	V	.	IV	III	II	III	IV	III	.

	44	43	42	41	45	5	7	3	2	10	17	16	15	14	13	12	6
C.																	
C Dactylorhiza traunsteineri	4	III		IV		*			*		*	II	II	*	*		
P Menyanthes trifoliata	5	V	5	III ²							*		IV	I			
C Drosera rotundifolia	5	III	5	IV							*		II	I	II	III	II
P Peucedanum palustre		II	4	I					o	*			II	I			
P Carex rostrata		II		II									II	*			
P Eriophorum angustifolium		*	5	*	II								II	*			
C Carex nigra			4	*	II	o			o		*	*	III	*	I		
C? Aulacomnium palustre											*	*	II		II ²		
D.																	
s Utricularia intermedia	4	III															
s Calliergon trifarium		IV	*	II													
s? Scirpus quinqueflorus	4	IV		II		o	*				I	*	*	*	*	*	
s Utricularia minor	5	IV			III						*	*	II				
s Scirpidium scorpioides	5 ⁴	V ⁴	*	V ³	V ⁴	V ⁴		*	IV ²	III	II		II	I	I	II	
s? Triglochin palustre					*	o				II			II	I	I	II	
Chara spp.													III				
E.																	
Ph Phragmites communis	4 ²	IV		V	II					*	I	*	II	I	III	II	III
Ph? Lycopodium europaeus		IV	*			o	*		*		I		II				
P? Hydrocotyle vulgaris			4					4 ²			*						
Ph Galium palustre				*		II			II	*	I	*	*		I		I
Ph Mentha aquatica						III			II	*			*		I	II	
P Juncus articulatus					*	o	o	o	o	I	I	II	III	II	II	II	
F.																	
T Eriophorum latifolium	*		5	*	II				o		II	II	III	III	*		
T Moerckia hibernica			5 ²	*				*	*		II	II	II	III	II	II	
T Pellia fabbronia							3	*			I	I	*	II	II	I	
T Tomenthypnum nitens				*						*		*	II	I ²	I		
T Dactylorhiza incarnata						o	o	o	o		*	I	II	I		I	
T Carex dioica	*	*						*			II			*	II	*	
G.																	
M? Gymnadenia conopsea				II	*				*	4	I	II	*	*	*		
M? Polygala amarella						*	o	5	II		III	III	*	II	*		
M? Carex flacca						o	4	5	*	*	IV	II	II	V	III	II	
M? Festuca rubra							2	*		*	*	I		II	II	*	
Ditrichum flexicaule											II	I		I			
m Galium boreale											I	II			I		
M Prunella vulgaris									*		II	II	*	III	II	*	
M? Briza media						*	*	*	*		I	I	*	IV	II	II	o
T Ctenidium molluscum									III ²		IV ³	V ⁴	III ²	V ⁴	V ³	V ³	V
H.																	
Leiocolea rutheana													II	I			
cc Leiocolea bantriensis	*		*										II	I		I	
Chiloscyphus pallescens			*										II	II			
T Riccardia multifida	*									*			III	I			
cc Cratoneuron filicinum						*					I	I	II	I	I	IV	*
cc Philonotis calcarea											*	I	IV	I	I	IV	
cc Cratoneuron commutatum									*		III	II	V ²	IV	IV	V ⁴	III
I.																	
M Angelica sylvestris													II	I	III	*	o
M Equisetum palustre	*			II						5	I	III	IV	III	III	IV	III
T Mnium seligeri	*			*					o		I	I ²	V	III	IV	IV	III
M Cirsium palustre			5	*	*			o	o		II	II	IV	III	V	IV	III
P? Calliergonella cuspidata			*	*		*	*	*	II	*	III	II	III	V ²	V ²	III	V
M Juncus subnodulosus													I	III	V	V	V
Equisetum arvense											I	*	*	II	I	III	III
M Galium uliginosum									o		*	I	II	I	I	I	*
m? Mnium rugicum											*	*	*	I	II	II	
f Eupatorium cannabinum															II	III	*
c Crepis paludosa													*	I	III	IV	*
M Deschampsia caespitosa															I	IV	*
f Cirsium oleraceum																III ²	
J.																	
T Riccardia sinuata			5 ²	*	*				o	*	I	I	II	I	IV	IV	V
R.																	
S? Cephalosia connivens	*		*	II						*			*	I	III		V
Calypogeia mülleri				*											III	I	V
Cephaloxiella spp				*											II	*	III
C Calypogeia fissa															II		III
L.																	
Alnus glutinosa			4						o				*			*	
Betula pubescens	*		4	III						4	I	*	II	IV	II		
Pinus sylvestris		II	*	IV	*	o	o		*	4	I	II	II	III			
Rhamnus frangula					IV	*	*		*				*	I			
Juniperus communis						o	2	o	II		IV	III	*				
Picea abies				II					*				I	II	V	*	

Cluster no.	44	43	42	41	45	5	7	3	2	18	17	16	15	14	13	12	6
Phanerophytes		1	7	4	<1			1	2	3	2	4	5	8	2	1	1
Nanophanerophytes	8	7	4	6	11	1	2	3	4	6	6	3	2	2	2		
Chamaephytes (dwarf shrubs)	13	12	11	12	10				1	9	2	2	3	2	2		
Chamaephytes (herbs)		1		3	2					3	2	<1	<1		<1		
Hemicryptophytes	32	37	46	39	58	78	82	77	70	62	64	61	58	64	68	78	71
Geophytes	23	19	16	21	12	9	5	10	11	13	15	21	22	20	18	15	24
Therophytes			<1		<1		11	6	7		5	5	<1	1	4	2	
Hydrophytes	24	25	15	15	5	5		3	5	4	4	3	9	3	4	4	4
Evergreen	7	10	5	15	8		2		5	8	4	5	6	6	1		2
Overwintering green	58	50	60	47	44	50	69	44	44	52	51	41	45	37	42	40	50
Summergreen	35	40	35	38	48	50	29	56	51	40	45	54	49	57	58	60	49
Hydromorphes	8	12	7	4	<1	4						1	3	<1	<1		
Helomorphes	50	49	53	52	50	62	45	53	44	47	43	34	50	44	54	50	61
Hygromorphes		2	2	2	<1	6	4	3	5	4	3	3	2	<1	2	6	2
Mesomorphes	12	13	18	15	16	8	27	15	21	23	31	34	24	24	25	19	11
Scleromorphes	22	19	15	25	34	19	14	27	26	25	22	25	18	29	17	22	24
Succulents	8	7	5	2	1	1	10	2	4	2	1	3	3	1	2	3	2
Scheuchzeria-Caricetalia nigrae	15	14	7	21	19	5		12	12	14	22	12	20	18	13	12	
Scheuchzeria-Caricetalia	23	19	24	12	6					5	3	4	8	3	2		
Rhynchosporion	12	5		2													
Tofieldietalia	6	9		10	15			16	9	8	9	4	12	6	9	17	
Eriophorum latifoliae	15	22	44	28	38	65	46	52	44	32	34	40	27	34	33	30	65
Oxycocco-Sphagnetes+Sphagnion	8	5	7	7	2					6			2	1	2	4	5
Sphagno-Utricularion	8	11		1		8					1	2					
Alnion			6														
Asteretalia+Plantaginietalia						6	35	12	5								
Phragmitetalia+Phragmitetalia	12	9	6	9	8					3	2	1	3	4	5	3	8
Magno-Caricion		4	6	4	4	8	4		7	5	2	1	2	1	2		
Molinio-Arrhenateretea							4		2	5	6	6	3	7	8	4	2
Molinietalia		1		2				4	2	8	2	1	6	1	6	8	8
Molinion				1	6	5	8		9	11	8	10	5	7	7	9	
Calthion															4	8	12
Vaccinio-Piceon				2					2				1		1		
Erico-Pinion													1	3	7	1	

Legend:

Clusters include relevés of following sites (Tyler 1979b): cluster 12: 1, 5, 6a, 6b, 7a, 7b; 13: 1, 2, 4, 6d, 8a, 9; 14: 32b, 38, 39, 40, 41, 42, 43, 45, 46a; 15: 37, 38, 39, 41, 45, 46a, 47; 16: 25b, 25c, 26, 27, 28, 31, 32b, 32c, 33a, 35, 36, 44a, 44b; 17: 12a, 12b, 14b, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24; 18: 48, 56; 2: 25c, 27, 30b, 34a, 34b, 44c; 3: 12b, 15; 41: 50, 52, 54, 55, 56, 57; 42: 13; 43: 49, 50, 51, 54; 44: 49, 52; 45: 28, 31a, 35, 48; 5: 30a, 33b, 34b; 6: 6c, 8b. Presence class V>80%, IV=80-61% etc. Occurrence in only one relevé: *; in stand only o. Characteristic C. Acidophilous or indifferent fen species. D. Calcareous puddle species. A-L: A. Character and differential species. B. General species. species. G. Drier-meadow species. H. Species of springs and flushes. E. Tall-sedges (swamp) species. F. Basiphilous fen of acid peat. L. Trees and shrubs. Letters in front of names of species refer to following syntaxa (Braun 1970, Oberdorfer 1957, Westhoff-Den Held 1969): a-Armerion maritima, ar-Agropyro-Rumiclon, c-Calthion, cc-Cratoneurion commutatum, C-Caricetalia nigrae, f-Filipendulion, m-Molinion, M-Molinietalia, N-Nardo-Callunetalia, O-Oxycocco-Sphagnetes, P-Parvocaricetalia, Ph-Phragmitetalia, s-Scorpidio-Utricularion, S-Scheuchzerietea, T-Tofieldietalia, 2-species occurs in several syntaxa. Number of excluded low-frequent species: 163. Indicator values of lifeforms, morphological forms and syntaxa according to Ellenberg (1974). Less fre-

Table 2. Schoenus phytocoena in S and SE Sweden.

Table 3. Summary of Schoenus phytocoena, their contact phytocoena, earlier investigations and successions.

Association/nucleus	Phytocoenon	No. Distribution area	Main species groups	Contact phytocoena	as	Earlier described by	Differences in species composition now/then	Presumed development towards
Oryzococcus-S. ferrugineus	Utricularia-Drepanocladus badius	44 Upland	Acidophilous, puddle, common mire	Scorpidium-Drepanocladus quagnaire/Selaginella-S. ferrugineus phytoc.	C. lasiocarpa-S. ferrugineus fen	Almqvist 1929	unknown	Selaginella-Pinus phytoc.
	Utricularia-Drepanocladus revolvens	43 -"-	-"-	-"-	-"-	-"-	-"-	- "-
	Selaginella-Pinus	41 -"-	Acidophilous, common mire	C. lasiocarpa; Utricularia-Drepanocladus phytoc./Myrica-Pinus fen	Myrica-S. ferrugineus fen? Pinus-Labrus-S. ferrug. woodland?	-"-	-"-	Myrica-Pinus or Labrus-Pinus phytoc.
	Sesleria-C. hostiana	45 Gotland	General	Cladium/Myrica-Pinus	Myrica-S. ferrugineus	Ljungqvist 1927	not distinct	?
	Riccardia-Moerchia	42 Öland	Acidophilous	Cladium/C. panicea-Scirpus hudsonianus	Cladium/C. panicea-Scirpus hudsonianus	Pettersson 1958	-"-	?
	Sesleria group, Myrica	18 Upland	Drier-meadow	Sesleria wet-meadow	S. ferrugineus sse.	-"-	-"-	Sesleria meadows
	-"- , C. hostiana	17 Öland	Drier-meadow	Chara; Cladium; Sesleria meadow/Sesleria meadow	S. ferrugineus	Ljungqvist 1929	not distinct	- "-
	-"- , Tofteldia	16 Gotland	-"-	Sesleria meadow/Sesleria meadow	-"-	Pettersson 1958	>Sesleria, Molinia, Juniperus, Ctenidium/>Scorpidium/C. hostiana	- "-
	Bartsia-Ophrys group, C. lepidocarpa	15 Östergötland	Spring, wet-meadow, basiphilous, indifferent	Cratoneuron/Scorpidium/C. lasiocarpa fens/Alnus-Betula carr	C. hostiana-S. ferrugineus community	Du Rietz 1961	>Molinia, C. flacca, Picea, Potentilla erecta/>C. hostiana	Molinia meadows or swampy woodlands
	Bartsia-Ophrys group	14 -"-	Basiphilous, drier-meadow	C. flacca-Molinia wet-meadow or Alnus-Betula carr	S. ferrugineus-Drepanocladus	Maidheim	wet-meadow, J. subnodulosus, acid peat/Scorpidium, bipartita	Molinia meadows or birch shrubs
	Calliergonella	13 Skåne	Wet-meadow	J. subnodulosus, C. lasiocarpa fens/Molinia wet-meadows	cladus intermedium mod. Schoenus communities	Maidheim 1943	wet-meadow, J. subnodulosus, Valeriana	
	Calliergonella					Maidheim 1949	Ctenidium, acid peat, less number of species	J. subnodulosus fens ?
	Valeriana group, C. lepidocarpa	12 -"-	Spring, wet-meadow	Cratoneuron/J. subnodulosus fens Molinia wet-meadows				
	Plasidena-S. nigricans	6 -"-	Acid peat, wet-meadow	Primula-S. ferrugineus/Molinia wet-meadow	Schoenus communities	Maidheim 1949	Ctenidium-domain, wet-meadow, acid peat/Drepanocladus-domain, C. lepidocarpa, and recolonisation?	
	Cladium-S. nigricans	5 Gotland	Swamp	Cladium/Primula-S. ferrugineus or S. interm.-S. ferrugineus	Cladium-S. nigricans	Ljungqvist 1927-29	Primula farinosa, less species	
	Glaux-S. nigricans	7 -"-	Seashore	Scirpus tobacummontani reed/S. intermedium-S. ferrugineus		Pettersson 1958	none	
	Glaux-S. ferrugineus	3 Öland	-"-	Blymus-Scirpus/Primula-S. ferrugineus			none	
	S. intermedium-S. ferrugineus	2 Gotland	Basiphilous	See cluster 5 and 7				

SCHOENUS VEGETATION AND ENVIRONMENTAL CONDITIONS
IN SOUTH AND SOUTHEAST SWEDEN

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Nomenclature is the same as in Tyler 1979 a.

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Introduction

In an earlier study the regional discontinuities within the vegetation of Schoenus-dominated wetland areas in South and Southeastern Sweden were described (Tyler 1979 a). By numerical methods two associations were distinguished, the Primula-Schoenus ferrugineus association mainly occurring in the provinces of Skåne, Öland, Östergötland and Gotland, and the Oxycoccus-Schoenus ferrugineus association of the province of Uppland. The Primula-Schoenus association was further divided into eight phytocoena arranged in three groups, and the Oxycoccus-Schoenus association into five phytocoena. Another five phytocoena, four of them characterized by Schoenus nigricans, were distinguished. In this study the vegetation is regarded as a continuum of species, the abundances of which are 'related to environmental factors by functions which are non-linear, often also non-monotonic and with zero values over part of the range' (Noy-Meir & Whittaker 1977:82).

The first objective is to establish if the observed variation in the vegetation is related to the variation in any of the investigated environmental variables, and to study the relative importance and interactions of these variables. The second objective is to characterize each phytocoenon, distinguished in Tyler (op. cit.) by environmental conditions.

In Sweden Witting (1947, 1948), Du Rietz (1949, 1954, 1959), Malmer & Sjörs (1955), Sjörs (1959, 1961) and Malmer (1962a), have studied environmental variables which are considered to be of importance for the differentiation of the plant cover in the vegetational gradient 'poor - rich' (e.g. Du Rietz 1949, Sjörs 1971, Trass & Malmer 1973). These variables include pH, calcium content and content of other mineral nutrients. Witting (op.cit.) and Du Rietz (1954) considered the calcium concentration to be the most important environmental variable for the variation: bog - poor

fen - rich fen - extremely rich fen vegetation. According to Sjörs (1952), the acid-base state is the main environmental gradient along which the vegetation of bog - poor fen - rich fen is distributed. He also stated that a 'high content of salts (at least of calcium carbonate) in the mire water is generally combined with rich fen vegetation but the latter is not always dependent on the former'. Calcium is considered largely to decide the composition of the vegetation (Sjörs 1971). The influence of other environmental factors (e.g. water movements) was stressed by Gorham (1952) and Malmer (1962 b, 1965) and also the importance of the amount per unit of time rather than instantaneous concentrations. Gorham concluded that the best method for studying mire vegetation in relation to environmental conditions is that of Tuomikoski (1942), i.e. the directions of variation, a method used by several Swedish mire (bog and fen) investigators (e.g. Sjörs 1948, 1950, Malmer 1962). An attempt to discriminate between bog - fen - marsh - swamp with regard to nutrients has also been made by Stanek et al. (1977), who concluded that Ca, P and N are best suited as discriminators. Fen and marsh were well separated from bog and swamp, but it was not possible to separate fen and marsh by soil chemical properties. Extremely rich fens, to which the *Schoenus* wetlands (sensu Tyler 1979a) belong, according to Waldheim & Weimark (1943) and Du Rietz (1949), have a high pH (>6.0 in soil water, Witting 1947, 1948; > 7.1 Sjörs 1952, Malmer 1965), a high concentration of calcium in soil water (>37 mg/litre, Du Rietz 1954), and a high CEC (cation exchange capacity), base saturation and total concentration of N and P in comparison to moderately rich fens (Sjörs 1961).

Values of pH stated in the literature for *Schoenus* vegetation from outside Sweden vary between 5.3 and 8.5 (mostly measured in water suspensions). Calcium carbonate content varies between 0.5 and 90 percent of dry soil matter (e.g. Zobrist 1935, Trass 1957, Langer 1958, Eicke-Jenne 1960, and Kask 1965). Few authors have studied CEC, organic carbon or humus

content, or available phosphate (e.g. Boeker 1957). Aluminium ions (Al^{3+}) in very low concentrations are toxic to Schoenus nigricans and Carex lepidocarpa from the British Isles (Clymo 1962, Sparling 1967). This may be the reason why they are restricted to sites with a high pH ('rich fens') or a low natural Al^{3+} concentration (bogs). Carex lepidocarpa also seems to require high concentrations of calcium ions. However, it is not known whether these findings are applicable to Swedish conditions.

Nowadays, directions of variation are often studied by ordination techniques, i.e. indirect gradient analysis, though the non-linear species response to the influence of environmental variables makes a careful study of these relationships necessary (Austin & Noy-Meir 1971). The interpretation of the principal axes of the species dimensional space as corresponding to axes of an environmental space (cf Beals 1973), may be replaced by an ordination of the environmental variables alone or in combination with the species as an approximation, at least of the vegetational space (Beals op.cit.), an ecosystemic ordination in the sense of Jeglum et al. (1971). Such a space is difficult to define because the environmental variables are not independent, and their effects on species synergetic. The variables are accordingly difficult to define, also as main factor complexes, and also difficult to measure in a manner corresponding to their influence on species. Owing to different scales of the environmental variables, their ordination requires standardization, the effect of which is thoroughly discussed by Noy-Meir et al. (1975). Only rather few authors have used ordination techniques on environmental variables (Ferrari et al. 1957, Bunce 1968, Goldsmith 1973, Bouxin 1975, 1976, and Gauch et al. 1976) or on the combination of species and environmental variables (Gittins 1969, Walker & Wehrhahn 1971). Of several ordination techniques, reciprocal averaging gives the ordination of stands and species which is least difficult to interpret in relation to environmental variables, according to Robertsson (1978), but not according to Gauch et al. (op. cit.).

Methods

Field and laboratory methods

Investigation area and vegetational data have been presented (Tyler 1979 a). Soil sampling was performed in most standard areas (size 4 m^2 , here called stands), used for vegetation sampling. After removal of the moss-layer in the interspaces, soil samples, representing the 0-10 cm level, were collected. Sometimes the ground was too stony to allow any sampling. Height of tussocks and thickness of the soil mixed with organic matter (in the following text called 'peat') were always estimated, the latter with a 2-metre probe. The samples were frozen as soon as possible, and thawed immediately prior to analysis.

pH was measured electrometrically directly in the fresh soil sample, if this consisted mainly of organic matter, or in a water suspension of fresh mineral soil (weight prop. 2:1) in the case of all samples from Öland and Gotland and a few from Östergötland. After removal of stones and living roots water content and dry (105°C) weight were estimated. From the fresh sample, the cations were extracted by leaching with neutral, molar $\text{NH}_4\text{OCOCH}_3$, and phosphate by 0.5 M NaHCO_3 (pH 8.5). Metal elements were determined by atomic absorption spectrophotometry (Ca, Mg, Fe, Mn) and flame photometry (Na, K) and phosphate by spectrophotometry using the ascorbic acid method according to Alexander & Robertsson (1970). Organic carbon was determined by the method of Tyurin (Kononova 1966), nitrogen by a semi-micro Kjeldahl procedure and carbonate titrimetrically according to Bundy & Bremner (1972). Finally, chloride ions were determined titrimetrically (Jackson 1958) in water extracts of a few samples.

Values of pH, estimated in water suspensions of carbonate rich soils, are considered minimum values, because percolation of CO_2 saturated water through soil (in situ) displaces

the $\text{CO}_3^{2-} - \text{HCO}_3^-$ equilibrium, especially important in rainy periods (Turner 1959). Seasonal variations occur, especially in soils where the buffer capacity is low (Ellenberg 1950, Lötschert & Ulrich 1961). Thus comparisons of pH values are uncertain, not only because different methods were used. Measurements performed in water suspensions give pH-values 0.80 ± 0.03 (n=20) units higher than measurements directly in fresh 'peat', according to my experience. Neutral $\text{NH}_4\text{OCOCH}_3$ partly dissolves the carbonates resulting in a certain over-estimation of exchangeable Ca and Mg and thus also overestimation of CEC. Alkaline NaHCO_3 is an extractant for phosphate, which shows good correlations with crop yields (Semb & Uhlén 1954, Enwezor 1977) and the L-ascorbic acid P-analyse method is the most precise according to John (1970).

Numerical analysis

The structure in the vegetational data was studied by principal coordinate analysis and reciprocal averaging. Principal coordinate analysis produces a matrix of weighted similarity coefficients, a Euclidean measure, which centers the unstandardized data by species (Orloci 1966, Gower 1966) (programme ORDINA, Roskam 1972). Only the stand ordination was performed. Centering means that the interest is concentrated 'on the differences in composition between sites only (not the absolute composition), and in the variance and covariance of species (not their cooccurrences or occurrences)' (Noy-Meir 1973). Further, the information is concentrated on the first few axes (Noy-Meir & Whittaker 1977). When unstandardized, quantitative data are used, the analysis is dominated by those species and those stands which have the highest totals (strictly $\sum x^2$ or variance) of the quantitative measure used (Noy-Meir et al. 1975). The quantitative measure in this study is the cover estimated according to the Hult-Sernander-Du Rietz scale (Trass & Malmer 1973) and expanded according to Tyler (1979 a).

Double standardization in reciprocal averaging, RA (Hill 1973), makes it possible to ordinate environmental and vegetational data in combination. Double standardization is considered a compromise between a site orientated and a species orientated model (Noy-Meir et al. 1975). Rare species in species poor sites (or extreme values of environmental variables) are overemphasized (ibid.). RA was applied to both vegetational and environmental data as well as to the combination of both. The method results in a non-centered, double-standardized, non-symmetric association matrix, the solution of which gives species and stand ordination simultaneously. Both species and stand scores are rescaled from 0 to 100 (Nichols 1977:194). The available RA programme performs the calculations described by Hill (op.cit., Appendix 2), which means that the eigenvalue is estimated, the percentage of total variance is not given, and the non-scaled eigenvector coefficients are not available. The axes obtained by RA are independent and non-orthogonal; thus the form of the species-dimensional space is unknown and the ordination plane of two orthogonal axes is arbitrary. Both numerical methods used are sensitive to nonlinearity and high β -diversity (Austin 1976 b).

Before calculating Pearson's product-moment correlation coefficients the normal distribution of environmental data was controlled (SPSS programme). All data except base saturation and phosphate concentration were found to be normally distributed.

Indicator values were calculated according to Ellenberg (1974) using the characteristic degree of cover (Malmer 1962 a) multiplied by presence as quantitative values per species (cf. Tyler 1979 a).

Results

Variation in vegetation

In the stand ordination (ORDINA) obtained from a selection of relevés and species, 90 relevés with odd numbers and 124 frequent species (the whole sample was too extensive for the available computer space), six principal axes were extracted. However, only the first three axes, together accounting for 34.4 percentage of the total variance, could be interpreted floristically. Stands with high positive scores on the first axis have no species, stands in the other end of that axis have eleven species in common, e.g. Schoenus ferrugineus, Primula farinosa, Parnassia palustris, Molinia coerulea, Campyllum stellatum and Drepanocladus revolvens. However, this principal axis roughly follows the number of species per stand, a consequence of the use of unstandardized, centered, quantitative data (Noy-Meir et al. 1975, cf. also Bates 1975 and Werger et al. 1978). The two ends of the second axis are characterized by Schoenus nigricans, Schoenus intermedius and Sesleria coerulea, and Myrica gale, Oxycoccus quadripetalus, Menyanthes trifoliata and Carex lasiocarpa respectively. On the third axis, stands with e.g. Juniperus communis and Carex hostiana are opposed to stands with Deschampsia caespitosa, Calliergonella cuspidata and Mnium seligeri.

On the plane of axes 1 and 2 stands with Schoenus ferrugineus are separated from those with Schoenus intermedius and nigricans (Fig. 1a). Some interference between Primula farinosa and Myrica gale is evident (Fig. 1b) but as a whole the stands are divided into a Schoenus nigricans group, an Oxycoccus-Schoenus ferrugineus group and a Primula-Schoenus ferrugineus group (the last-mentioned richest in species). Since the distances from origin are greater for stands of the first two groups, the variances of these stands are best accounted for. These stands are closer related to the first two principal

axes than are stands of the Primula-Schoenus group. This group is not strictly divided into subgroups by the differential species Sesleria coerulea, Valeriana dioica, Bartsia alpina and Ophrys insectifera (cf Tyler 1979 a) whereas Carex limosa has delimited occurrences within the Myrica-Schoenus group (Fig. 1c). The pattern in this plane mainly demonstrates the variation in species cover in all stands around the centroid (the average cover, cf. Noy-Meir 1973).

RA was applied to all 189 relevés and a selection of 149 species. The four axes extracted are all bipolar. The first axis has seashore species and wet mire species on opposite ends (Fig. 2) and most species gathered within a range of 25-40 percent of the total length of the axis. It is in fact a gradient between two endpoints with rare species occurring in species-poor stands, a situation produced by the double standardization (Noy-Meir et al. 1975). Also on axes 2 to 4 the seashore species are placed at the one end, while species typical of each axis occupy the other end (Figs. 2, 3). On the fourth axis Cladium mariscus, Schoenus nigricans and Calypogeia species are their counterparts. Typical RA-patterns of species (or stands) appear as an angle in plane 1/2 and a 'sinusoid' curve in plane 1/3 (cf. Werger et al. 1978).

It is difficult to summarize these different species gradients in a simple pattern. The non-linear species response to one environmental factor complex seems to result in a horse-shoe shaped pattern of stand groupings (cf. e.g. Noy-Meir-Austin 1970, Noy-Meir & Whittaker 1977). Several authors have tried to relate the principal axes to such factor complexes or even to single factors (cf. Noy-Meir & Whittaker op. cit.), but these axes 'have a precise definition as certain linear combinations of species' and only 'under certain situations, there may be a nearly linear relation between the first principal component axis and an underlying environmental gradient' (Nichols 1977:194). The double standardization of RA is one of the three situations discussed by Nichols where a 'quasi-

linear axis-to-gradient relation' may be possible. A horse shoe shape passing through most stand constellations in the first ORDINA plane may reasonably be presumed though some intermediate stands near the origin are left out. The horse shoe of ORDINA and angle of RA are related, because a turn 90° anti-clockwise of the first RA-plane results in a pattern similar to the horse shoe, though less involuted. Unless the axes of ORDINA are rotated, gradients extend along the diagonals of the plane (cf. Gittins 1969).

It seems to be possible to interpret the ORDINA ordination very roughly in terms of a moisture complex gradient, according to the species distributions, e.g., in Fig. 1 d and e. According to my field experience, a moisture factor complex may also be related to the whole length of the RA 'sinusoid' curve, though in such a way that a drop in general soil water level relates to the left line, a drop in summer water level to the perpendicular line, and the difference between land and seashore to the right line. However, both in ORDINA and RA it may be possible to relate several other environmental factor complexes to the species (or stand) gradients. In some of the Schoenus nigricans stands Glaux maritima occurs (seashores), in others Cladium mariscus (lake shores with calcareous mineral soil). Oxycoccus quadripetalus indicates a high content of organic matter in the soil and Cirium oleraceum a not too nutrient-poor soil (Landolt 1977) (Fig. 1 f). Thus the distribution of the vegetation along a complex moisture gradient is probable, though other gradients, e.g. content of organic matter, carbonate and nutrients, are also possible for the interpretation.

Variation in environment

Pairwise plotting of the twelve normally distributed environmental variables showed relationships of logarithmic, hyperbolic and linear functions. Appropriate transformations resulted in linear relationships between most variables. The

environmental variables were distributed over two groups (the carbon and the carbonate groupings), the members of which were negatively correlated (Fig. 4). However, some of these relationships depend on action of the same not-measured environmental variable, e.g. 'peat'-thickness and organic carbon (C), or are different ways of expressing almost the same environmental property, e.g. calcium saturation (Ca) and CEC.

The two groupings can also be recognized on the axes of the RA-ordinations. All fourteen environmental variables were ordinated and the effect on the ordination of some of these variables was studied by the exclusion of one, two or several of them. 'Peat'-thickness and dry weight are placed at the opposite ends of axis 1 in all ordinations where 'peat'-thickness is included (Table 1). This is due to the many zero values of 'peat'-thickness, which make this attribute outstanding, but it also implies that the two groupings of variables are separated. The mutual order of the variables on axis 1 is the same in all ordinations (Table 1, Fig. 5). This order reflects the correlations within the carbon but not within the carbonate grouping. The first axis in all ordinations separates the carbon and the carbonate-groupings and the following axes distinguish stands aberrant with respect to a certain environmental variable, e.g. available phosphate (P) or the calcium:magnesium ratio (Ca:Mg). The variable sequence dry weight to tussock, on axis 3 of ordinations 2 and 3 (Table 1), is found again in Fig. 4, though not in accordance with the highest correlation coefficients within the carbonate grouping. The variable 'height of tussocks' does not account for any part of the variability. From Table 1 and Fig. 5 it is clear that pH, base saturation and Ca saturation are closely related on almost all axes in every ordination. If pH is <6.8 then base saturation is <95 percent and Ca content <90 percent. The correlation between pH and Ca is average ($r = 0.58^{***}$) but higher ($r = 0.75^{***}$) if the magnesium-rich

samples are excluded (cf. Steele 1955, Bunce 1968).

From the results of all ordinations the following order of importance of the environmental variables may be obtained: 'peat'-thickness > dry weight > P > C > CO₃ > Ca:Mg > pH > water content > N. The variance of each of these variables is not accounted for by one axis only. Replacement of the zero values of 'peat'-thickness with the arbitrary value 1 mm, or calculation of carbonate content on a volume basis, would not have altered the order of importance. However, the values of C would have been much less extreme in the stands with the highest C percentage of the dry weight, if calculated on a volume basis, and this variable would perhaps have been ranked lower. Each of the environmental variables mentioned represents directions of variation, though some of them are opposites in the same direction of variation.

The significant variables of axis 1 in ordination 2, 'peat'-thickness and dry weight, have smooth isolines on the plane of axes 1 and 3 (Fig. 6A,B) while on the same plane, organic C, an important variable of axis 3, shows less smooth isolines (Fig. 6C). In the same way CO₃ and Ca:Mg are evenly distributed over the plane of axes 1 and 2 of ordination 5 (Fig. 6D,E).

Relationships between vegetation and environment

Co-ordination

One of the most differentiating environmental variables, C, plotted on the ORDINA-plane of axes 1 and 2, shows no perfect co-variation with any of the two diagonals, though most stands with highly organic soils belong to the Oxycoccus-Schoenus ferrugineus group, and several stands with almost pure mineral soil to the Schoenus nigricans group (Fig. 7A). In fact, none of the environmental variables studied co-variate in a satisfactory way with the vegetation either

along the axes or diagonally over the ordination plane obtained by ORDINA. Nor are any smooth gradients obtained when environmental variables are plotted on the stand ordination of RA, but there are interesting patterns. A high dry weight and no presence of 'peat' characterize the soils of stands from seashores and swamps, a low dry weight the wet mire stands (Fig. 7 B,C). Almost all stands along the longitudinal part of the pattern in Fig. 7D (RA, axes 1,3) have at least some carbonate in the soil. The plotting of environmental variables on the vegetation ordination is of little help for searching for main gradients in this study.

Species determine all four axes of ordination 6, which includes both selected species and the environmental variables (Table 1). Species arrangement on the planes of ordination is closely related to that on the planes of the pure species ordinations, though the patterns are more constricted and smoothed out (Fig. 8, 9). Furthermore, the environmental variables are ordered in the same way as when ordinated separately (cf. ordinations 1 and 6, Table 1). Smooth isolines are obtained when 'peat'-thickness and dry weight are plotted on the plane of axes 1 and 4 of stand ordination 6 (Fig. 10 B,C), more winding isolines, despite distinct gradients, when P and C are plotted (the first variable on plane 1/2, Fig. 10 A,D. Plotting of CO_3 on the plane of axes 1 and 4 results in a more complicated pattern (Fig. 10 E).

Between vegetation and the environmental variables studied the association is clear. High values on 'peat'-thickness C and C:N are associated with a Schoenus vegetation, where Myrica gale and Oxycoccus quadripetalus occur, high values of P with a vegetation of Juncus subnodulosus, Valeriana dioica and Carex lepidocarpa, high values of CO_3 and Ca:Mg with Calamagrostis varia, Juniperus communis and Sesleria coerulea, and finally, high values of dry weight and low values of Ca:Mg with Schoenus intermedius, Carex pulchella, and Triglochin maritimum (Fig. 8,9). Thus the Schoenus

vegetation is distributed along those directions of variation which were obtained at the ordination of environmental variables. The first and main direction is associated with the factor complex of soil material, the carbon grouping versus the carbonate grouping, and the second with a nutrient factor complex, represented by available phosphate versus Ca:Mg. Other directions of variation cannot be demonstrated by combined ordination unless a selection of species, stands and environmental variables is made.

Ordination versus classification

Some phytocoena discussed by Tyler (1979 a) are well distinguished in the first plane of the ORDINA stand ordination, while others are not, i.e. nos 12-14, 16 and 17 (Fig. 11 A). The first plane of RA is in this respect equal to that of ORDINA (Fig. 11 B). In the second plane of RA (Fig. 11 C), however, all but two phytocoena, no 16 and 17, are easy to delimit, though few are represented by stand groupings separated distinctly. Stand ordination of species and environmental variables in combination gives patterns of stands which are less distinctly related to the TABORD classification (Fig. 11 F). The sequences of phytocoena obtained by the TABORD-classifications (in numerical order) are recovered neither by the ORDINA nor by the RA ordinations, since the TABORD sequences are one-dimensional pictures of multidimensional relations. However, this statement is not valid for the subdivisions of the Oxycoccus Schoenus association.

Environmental characterization of phytocoena

The variation of the environmental variables within each phytocoenon is not insignificant (Table 2, compare Fig. 11 D, E, F with Fig. 6 A-E and Fig. 10 A). Most of this dispersion refers to variation in site conditions, since the error in sampling and analysis amounts to a mean of <5 percent, except

for the P analysis, where it is <15 percent. Subunits within one phytocoenon often differ considerably in one or several environmental variables (cf. Tyler 1979 b).

It is obvious that the site conditions of the Oxycoccus-Schoenus association and the Primula-Schoenus association differ in almost all respects. The carbon grouping is typical for the Oxycoccus-Schoenus association and the carbonate grouping for the Primula-Schoenus association. Not only is the relation between C and dry weight inverse and the regression function logarithmic but the Oxycoccus-Schoenus association is well separated from other phytocoena along the regression line, too (Fig. 12). Phytocoena occurring on Öland and Gotland are also placed at the distal end, regardless of dominating Schoenus species, and those of Skåne and Östergötland are intermediate in position. Most phytocoena of the Oxycoccus-Schoenus ass. and some of the Primula-Schoenus ass. are distributed along a distinct moisture gradient, calculated according to Ellenberg (1974) (Fig. 11 C). The degree of litter decomposition is distinctly lower in the Oxycoccus-Schoenus ass. than in the Primula-Schoenus ass., as is shown by the higher C:N rate. However, the amount of C per volume of intact soil is lower in the Oxycoccus-Schoenus ass. (except the Sesleria-C. hostiana phytocoenon) than in several phytocoena of the Primula-Schoenus ass. with a lower C:N. Hence, both the production and the decomposition of organic matter seem to be low in the Oxycoccus-Schoenus ass. The acidophilous and common mire species (cf. Tyler 1979 a) seem to be related to the carbon grouping. Within the Oxycoccus-Schoenus ass. the Sesleria phytocoenon is most aberrant and most similar to phytocoena within the Primula-Schoenus ass., and the opposite is true of the Myrica phytocoenon. Lack of sufficient data from Sweden makes comparisons impossible while the pH values given by Trass (1957) and Kask (1965) for Myrica-Schoenus phytocoena are lower than those of the present study. The pH range given by Mörn sjö (1969) for South Swedish Carex elata-Utricularia communities is the

same as that for the Utricularia-Drepanocladus phytocoena.

An exceptionally high Ca:Mg ratio is typical of the *Carex hostiana* phytocoenon, a high CO₃ content of the *Tofieldia* phytocoenon, probably due to different maternal soil material. Drier-meadow species are typical of these phytocoena (cf. Tyler 1979 b). The carbonate content and pH of these stands agree closely with those of Schoenetum nigricantis typicum given by Zobrist (1935). Corresponding values for a Primulo-Schoenetum with Tofieldia calyculata and Sesleria coerulea in Continental Europe have a much wider range (Eicke- Jenne 1960). The Carex lepidocarpa (Valeriana), the Fissidens-Schoenus nigricans, and the Cladium-Schoenus nigricans phytocoena are all distinguished by their high concentration of available P. However, the estimation of available phosphate gives the instantaneous concentration and gives no information about the mobilization rate. The Carex lepidocarpa (Valeriana) phytocoenon also has the lowest contents of exchangeable and dissolved potassium within the Primula-Schoenus association on the sampling occasions. Several of the tall herb species (e.g. Cirsium oleraceum, Filipendula ulmaria) in this phytocoenon are considered by Ellenberg (1952:75) to occur in potassium-poor but phosphate-rich sites. The 'nitrogen figure' (Ellenberg 1974) is the highest represented in this study (3.0 compared to 2.5 in all other phytocoena). One sample of the Cladium-phytocoenon had an extremely high concentration of P (scored 100 on axis 2 of ordination 6) maybe due to bird droppings. Wet-meadow and swamp species are typical of the sites richest in P. Valeriana dioica, Phragmites communis, Filipendula ulmaria and Angelica sylvestris, i.a., also occur in the Schoenetum schoenetosum ferruginei of Zobrist (1935) and certain environmental variables reported by him (pH, CO₃, C) differ rather little from those of the Valeriana group in the present study. The content of available P (per g dried soil) in a Schoenus ferrugineus vegetation

with Valeriana dioica and several Molinietales-species in Germany (Boeker 1957) was about three times higher than the content in stands of the C. lepidocarpa phytocoenon of the Valeriana group. As an average, much higher values of several environmental variables than those given for extremely rich fens (Sjörs 1971) are typical of the Primula-Schoenus ass.

The Glaux, Cladium and Schoenus intermedius-phytocoena all occur on nearly pure mineral soils with a high pH. pH values are much higher than those given by Zobrist (1935) and Eicke-Jenne (1960) for Cladietum. The Glaux phytocoena have typically a low Ca:Mg and low but measurable contents of chloride (≤ 0.3 percent in soil water).

Conclusions

There are close connections between Schoenus phytocoena and some environmental variables. The phytocoena are separated according to variables related to the soil material and the nutrient factor complexes. The soil in this case is a peat (sensu Kubiena 1953), or a muck (Anmoor, cf. Göttlich 1965), but may also be almost purely mineral. The main difference is between phytocoenoses of sites with peat-formation and of sites with slight or no peat-formation, e.g. the carbon and the carbonate groupings. However, a prerequisite of peat or muck formation is a certain interaction between hydrological conditions and vegetation. In my opinion, the hydrological conditions must be regarded as the most important environmental factor complex operating on the different Schoenus phytocoenoses. Stagnant soil water in depressions as well as water oozing or welling from bedrock and superficial deposits above or just below the surface of the ground (topogenous and soligenous soil water according to Sjörs 1948), gives rise to wetlands with a constantly or temporarily high water table. Deficiency of oxygen caused by permanently stagnant water is a prerequisite for the peat-formation of wetlands with Oxycoccus-Schoenus phytocoenoses (Table 3). The peat

deposits diminish the transport of calcium and other ions from the underlying mineral soil of the depressions or from the surrounding ground. As time goes on such a fen site becomes less rich in calcium and the vegetation changes into a less basiphilous type. In shallow depressions and where the water oozes from a superficial source, the water table may stay well below the surface of the ground in summer but at or above the surface from late autumn to late spring. Sometimes recurrent lakes (Sw. vätar) arise. Precipitation of lake marl, and probably a rapid decomposition of the litter is typical of such sites on Gotland and Öland, the distribution area of the *Tofieldia* and the *Carex hostiana* phytocoena. A flow of soligeneous calcareous water supplies the sites with Ca, CO₃ and nutrients continuously. The waterlogged conditions cause incomplete decomposition but the organic matter is mixed with mineral soil and precipitations of tufa, i.e. muck. Phytocoenoses of the Bartsia-Ophrys and the Valeriana groups occur on such sites, but sometimes also those of the *Sesleria* group.

The first direction of variation, though associated with variation in soil material, is thus more to be looked upon as a variation in hydrological conditions. This conclusion is confirmed by the ordination result (cf. Table 3 with Fig. 11 A-C). The ordinations of species and environmental variables in combination and the corresponding stand ordinations may be explained in terms of both moisture conditions and other environmental variables studied.

The second direction of variation is associated with the nutrient factor complex, though not independent of hydrological conditions. Flushing water implies a continuous supply of nutrients but also a supply of fine mineral particles which make the organic matter less water-permeable. According to Göttlich (1965) the physical properties of the Feinkorn-Anmoor counteract the favourable influence of the better nutrient supply. Though only nutrient flow and uptake per

unit of time can give information about the real nutrient state of the phytocoenoses, it seems probable that the Carex lepidocarpa phytocoenon of the Valeriana group is developed in sites with a higher nutrient state than most other Schoenus phytocoena, to judge from the estimated content of available phosphate.

Further directions of variation are associated with the CO_3 content and the Ca:Mg ratio. Calcium and/or magnesium carbonate influence the physical and chemical properties of soils in a complicated way. pH higher than 7 and a very high content of either of these two cations may suppress the availability of several other plant mineral nutrients. Thus these directions of variation are parallell to the nutrient factor complex. The conclusions of Witting (1947, 1948), Du Rietz (1954), Sjörs (1952, 1971) that Ca-content, pH, acid-base state and content of minerals are important environmental variables and useful as discriminators between different fen types are partly verified in the present study. However, this study further shows that distinct gradients occur within the extremely rich fens and that hydrological conditions play a crucial role for the differentiation.

Summary

The relations between the Schoenus phytocoena and their site conditions are elucidated by stand and species ordinations (ORDINA, RA) and by comparisons of ordinations of environmental variables alone and ordination of the combined environmental and species variables (RA). Correlations between the environmental variables show that they may be gathered into two contrasting groups, the carbon and the carbonate groupings, respectively. This first direction of variation is related to hydrological conditions causing the differences in thickness of organic soils, content of organic carbon and dry weight of intact soil per unit volume. The second direction of variation is associated with a nutrient factor complex, in this

study represented by available phosphate.

The carbon grouping and a constantly high level of mainly topogeneous soil water is typical of sites of the Oxycoccus-Schoenus association. The Sesleria group of the Primula-Schoenus association is related to sites with a periodically low table of topogeneous or soligeneous soil water and mineral or mucky soils with high values of carbonate content, pH and CEC and a fairly low nutrient state, while the sites of the Bartsia-Ophrys and Valeriana groups have a fairly high level of mainly soligeneous soil water and mucky soils with variable carbonate content, intermediate pH and CEC and somewhat higher nutrient state. Periodically flooded sites with topogeneous soil water and mineral soils are typical of the Cladium-Schoenus nigricans, Schoenus intermedius-Schoenus ferrugineus and Glaux phytocoena.

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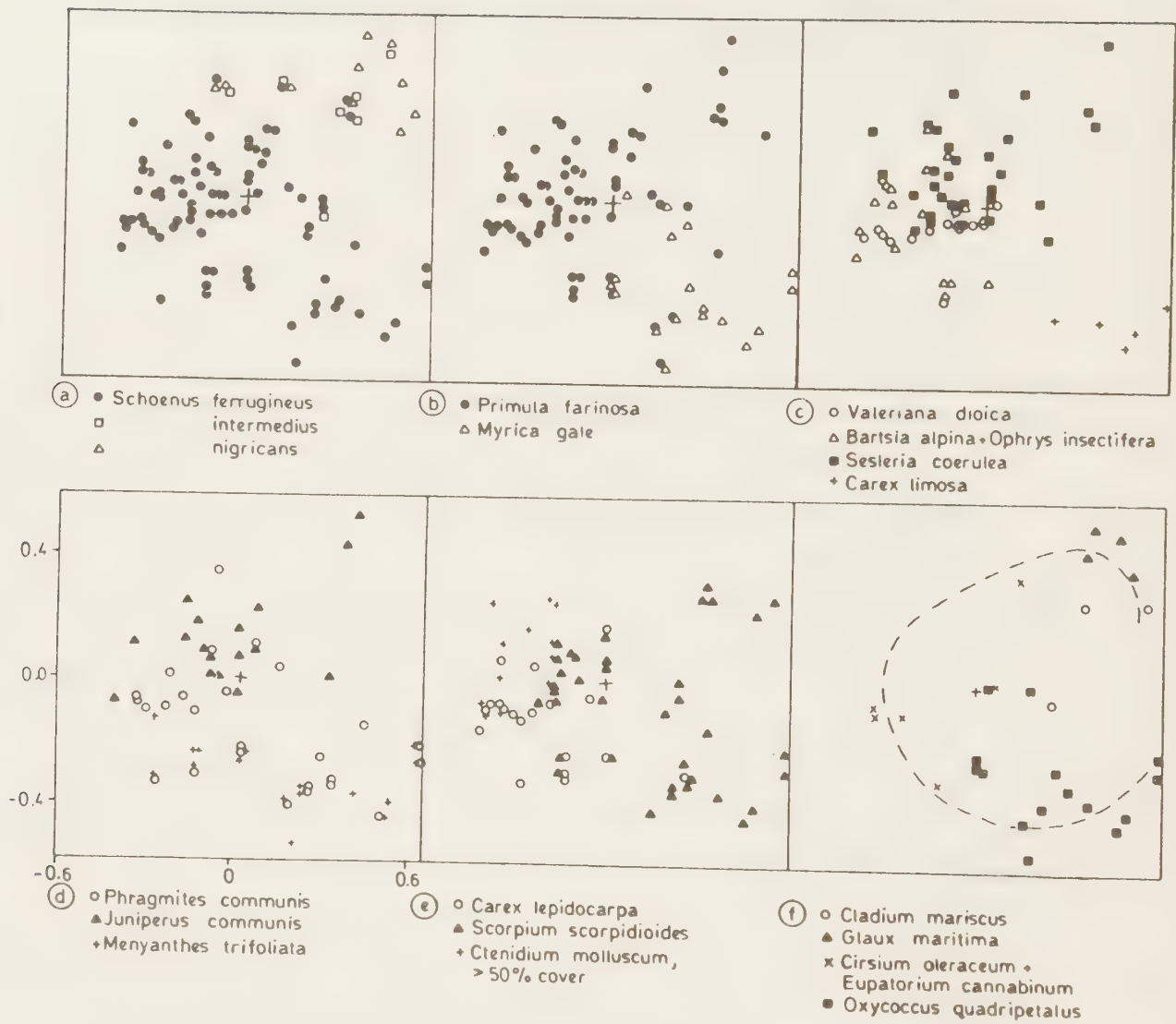


Fig. 1. Species distribution on the ORDINA stand ordination. Plane of axes 1 and 2, percentage extracted variance 15 and 11 respectively.



Fig. 2. Species ordination, RA, plane of axes 1 and 2.

Estimated eigenvalues: axis 1 0.39, axis 2 0.33.

Abbreviation of the species names see below.

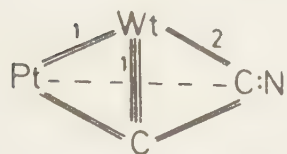
Acpt Achillea ptarmica
Algl Alnus glutinosa
Ansy Angelica sylvestris
Anpo Andromeda polifolia
Aupa Aulacomnium palustre
Bapu Betula pubescens
Beve Betula verrucosa
Brme Briza media
Brme Bryum nuxiamense
Brps Bryum pseudotriquetrum
Cacu Calliergonella cuspidata
Cadio Carex dioica
Cadis Carex distans
Cael Carex elata
Caelo Campylopus elodes
Cafi Calypogeia fissa
Cafi Carex flacca
Caho Carex hostiana
Cala Carex lasiocarpa
Cale Carex lepidocarpa
Cali Carex limosa
Camu Calypogeia mulleriana
Capa Carex panicea
Capo Campylopus polygamus
Capr Cardamine pratensis
Capu Carex pulchella
Cari Carex nigra
Caro Carex rostrata
Cast Campylopus stellatus
Catr Calliergon trifarium
Cava Calamagrostis varia
Coco Cephalozia connivens
Celi Centaurium litorale
Ceph Cephalozia species
Chpa Chiloscyphus pallens

Ciol Cirsium oleraceum
Cipa Cirsium palustre
Cist Clinidium stygium
Cima Cladium mariscus
Croo Cratoneuron commutatum
Crfi Cratoneuron filicinum
Crpa Crepis paludosa
Ctno Ctenidium molluscum
Dacr Dactylorhiza cruenta
Dain Dactylorhiza incarnata
Dacc Dactylorhiza ochroleuca
Datr Dactylorhiza traubsteineri
Deca Deschampsia caespitosa
Difi Ditrichum flexicaule
Dran Drosera anglica
Drba Drepanocladus badius
Drro Drepanocladus revolvens
Eppa Epipactis palustris
Eqar Equisetum arvense
Eqfl Equisetum fluviatile
Eqpa Equisetum palustre
Eqva Equisetum variegatum
Eran Eriophorum angustifolium
Eral Eriophorum latifolium
Eupa Eupatorium cannabinum
Fear Festuca arundinacea
Feov Festuca ovina
Feru Festuca rubra
Fiad Fissidens adianthoides
Fios Fissidens osmundoides
Fiul Filipendula ulmaria
Frax Fraxinus excelsior
Gabo Galium boreale
Gapa Galium palustre

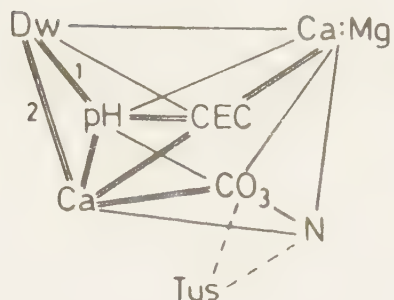
Gaul Galium uliginosum
Gma Glaux maritima
Gylo Gymnadenia conopsea
Gyod Gymnadenia odoratissima
Hyvu Hydrocotyle vulgaris
Jual Juncus alpinus
Juar Juncus articulatus
Jubu Juncus bulbosus
Jucm Juniperus communis
Juma Juncus maritimus
Jusu Juncus subnodulosus
Leba Leontodon autumnalis
Leba Leiocolea bantriensis
Lehi Leontodon hispidus
Leru Leiocolea rutheana
Lica Linum catharticum
Lohe Lophocolea heterophylla
Lyeu Lycopus europaeus
Lysa Lythrum salicaria
Meat Mentha arvensis
Meat Mentha aquatica
Metr Menyanthes trifoliata
Mnps Mnium pseudopunctatum
Mnru Mnium rugicum
Mnse Mnium seligeri
Moco Molinia caerulea
Mofi Moerckia flotoxiana
Mqga Myrica gale
Opin Ophrys insectifera
Oxru Oxycoccus quadripetalus
Pefa Pellia fahroniana
Pepa Pedicularis palustris
Peupa Peucedanum palustre
Phca Philonotis calcarea
Phco Phragmites communis

Piab Picea abies
Pial Pinguicula alpina
Pisy Pinus sylvestris
Pivu Pinguicula vulgaris
Plma Plantago maritima
Poan Potentilla anserina
Poer Potentilla erecta
Prfa Primula farinosa
Prju Preissia quadrata
Pum Polygala amarella
Rhfr Rhamnus frangula
Rhfr Rhytidadelphus triquetrum
Rimu Riccardia multifida
Ridi Riccardia pinovis
Risi Riccardia sinuata
Sape Salix pentandra
Sfe Schoenus ferrugineus
Schu Scirpus hudsonianus
Schum Scorzonera humilis
Scin Schoenus intermedius
Scni Schoenus nigricans
Sogu Scirpus multinervosus
Scsc Scorpidium scoroidioides
Scun Scirpus uniglumis
Seoc Seleria coerulesa
Sese Selaginella selaginoides
Supr Succisa pratensis
Tavu Taraxacum vulgare
Tema Tetranolobus maritimus
Toca Tofieldia calyculata
Toni Tomenthinum nitens
Trma Triglochin maritimum
Trpa Triglochin palustre
Tufa Tussilago farfara
Utin Utricularia intermedia
Utm Utricularia minor
Vadi Valeriana dioica

Positive relations
carbon-grouping

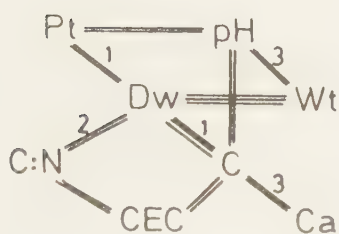


carbonate-grouping



- 1) $\log Pt, \log C$
 $\log Dw, \log CEC,$
 $\log CO_3$
- 2) $\frac{1}{C:N} \quad r = -$
 $\frac{1}{Dw} \quad r = -$

Negative relations



- 1) $\log Pt, \log Dw$
- 2) $\frac{1}{Dw} \quad r = +$
- 3) Curved relation
untransformed,
best-fitting line

- $\equiv r \geq 0.75$
 $\equiv r = 0.50 - 0.74$
 $\equiv r = 0.25 - 0.49$
 $\equiv r < 0.25$

Fig. 4. Correlations between the environmental variables.
Significance level $p = 0.001$. $N = 173$. Symbols
same as in Table 1.

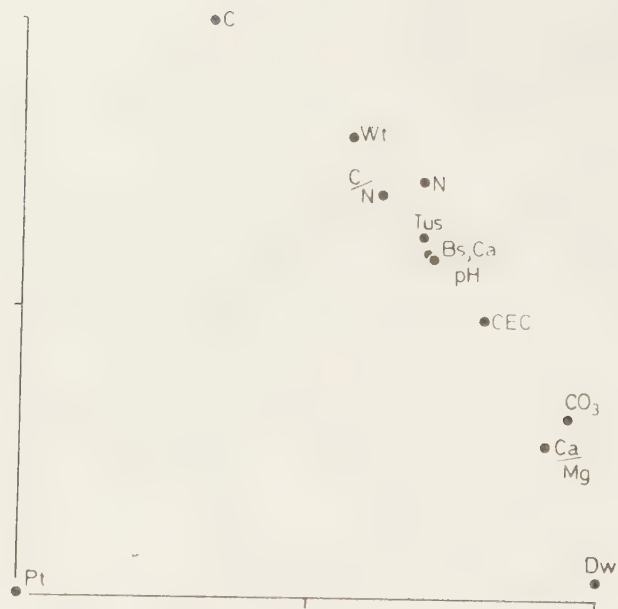


Fig. 5. Environmental variables on the plane of axes 1 and 4, ordination 1 (cf. Table 1).

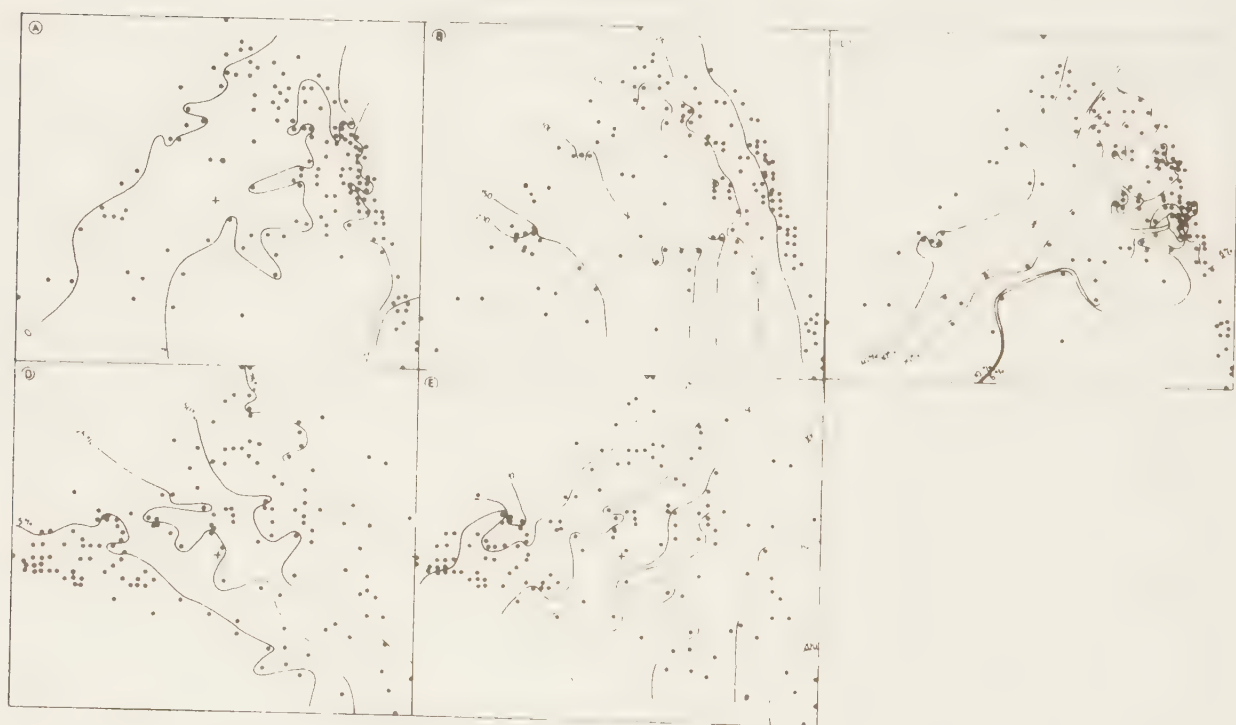


Fig. 6. Gradients of environmental variables on planes of ordinations 2 and 5 (cf. Table 1).

- A. Dry weight, kg/dm^3 , ordination 2, axes 1 and 3.
- B. 'Peat'-thickness, cm, ordination 2, axes 1 and 3.
- C. Organic carbon, percent of dry weight, ordination 2, axes 1 and 3.
- D. Carbonate, percent of dry weight, ordination 5, axes 1 and 2.
- E. Ca:Mg, ordination 5, axes 1 and 2.



Fig. 7. Plot of environmental variables on stand ordinations, ORDINA and RA.

A. Organic carbon, percent of dry weight, ORDINA, plane of axes 1 and 2.

B. 'Peat'-thickness, cm, RA, plane of axes 1 and 2.

C. Dry weight, g:10 /dm³, RA, plane of axes 1 and 2.

D. Carbonate, percent of dry weight, RA, axes 1 and 2.



Fig. 8. Ordination of species and environmental variables in combination, plane of axes 1 and 2. Selected species..



Fig. 9. Same as Fig. 8, but plane of axes 1 and 4.

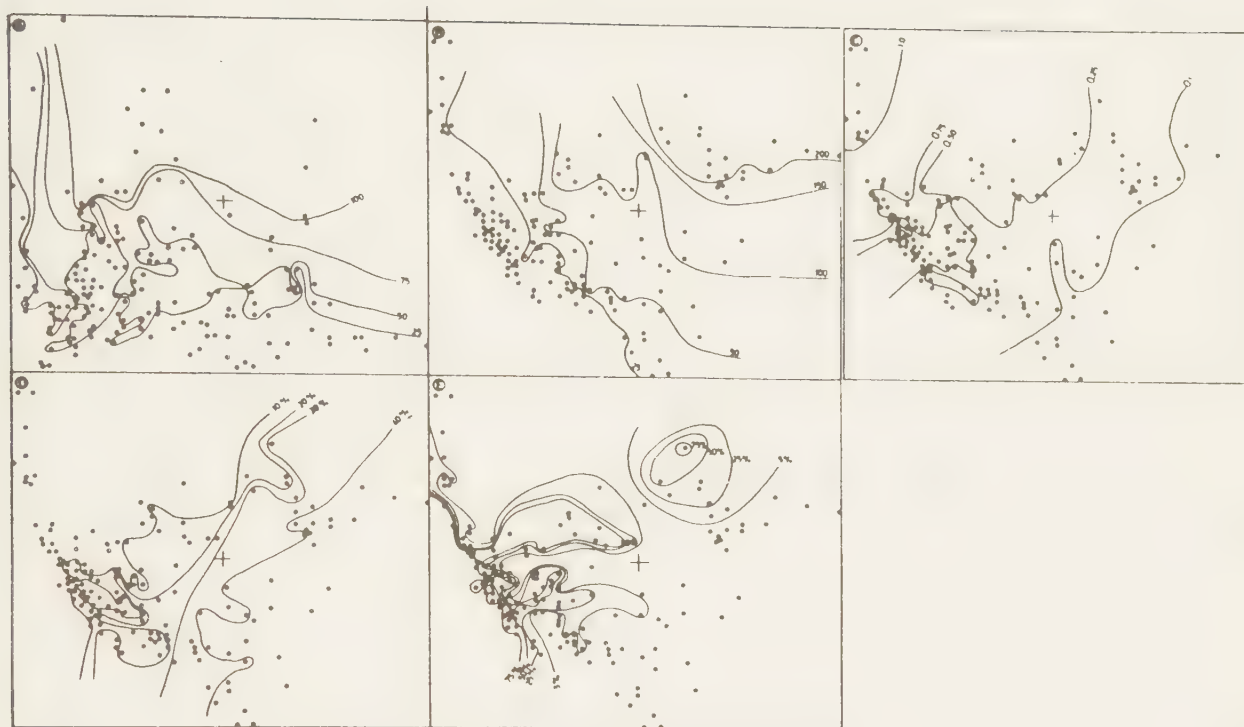


Fig. 10. Gradients of environmental variables on planes of ordination 6 (cf. Table 1)

- A. Phosphate, $\mu\text{mol}/\text{dm}^3$, axes 1 and 2.
- B. 'Peat'-thickness, cm, axes 1 and 4.
- C. Dry weight, kg/dm^3 , axes 1 and 4.
- D. Organic carbon, percent of dry weight, axes 1 and 4.
- E. Carbonate, percent of dry weight, axes 1 and 4.

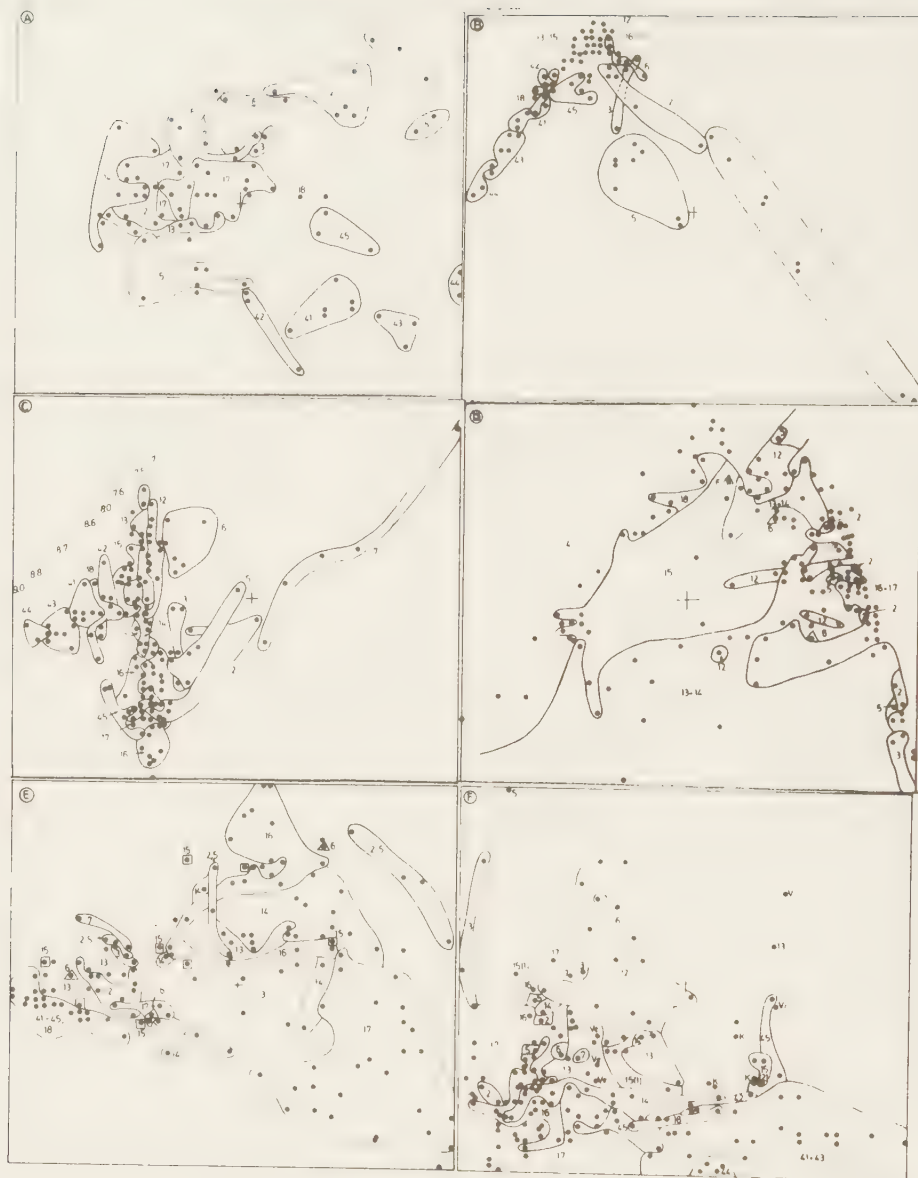


Fig. 11. Plot of TABORD clusters on planes of stand ordinations. A. ORDINA, plane 1/2. B. RA, plane 1/2. C. RA, plane 1/3. The numerals above the phytocoenon numbers are moisture indicator values according to Ellenberg. D. Ordination 2, plane 1/3. E. Ordination 5, plane 1/2. F. Ordination 6, plane 1/2. For phytocoenon numbers see Table 2. K = Kärna mosse, Ve = Vejla sjö, Vi = Vittskövle, cf. Tyler (1979 b).

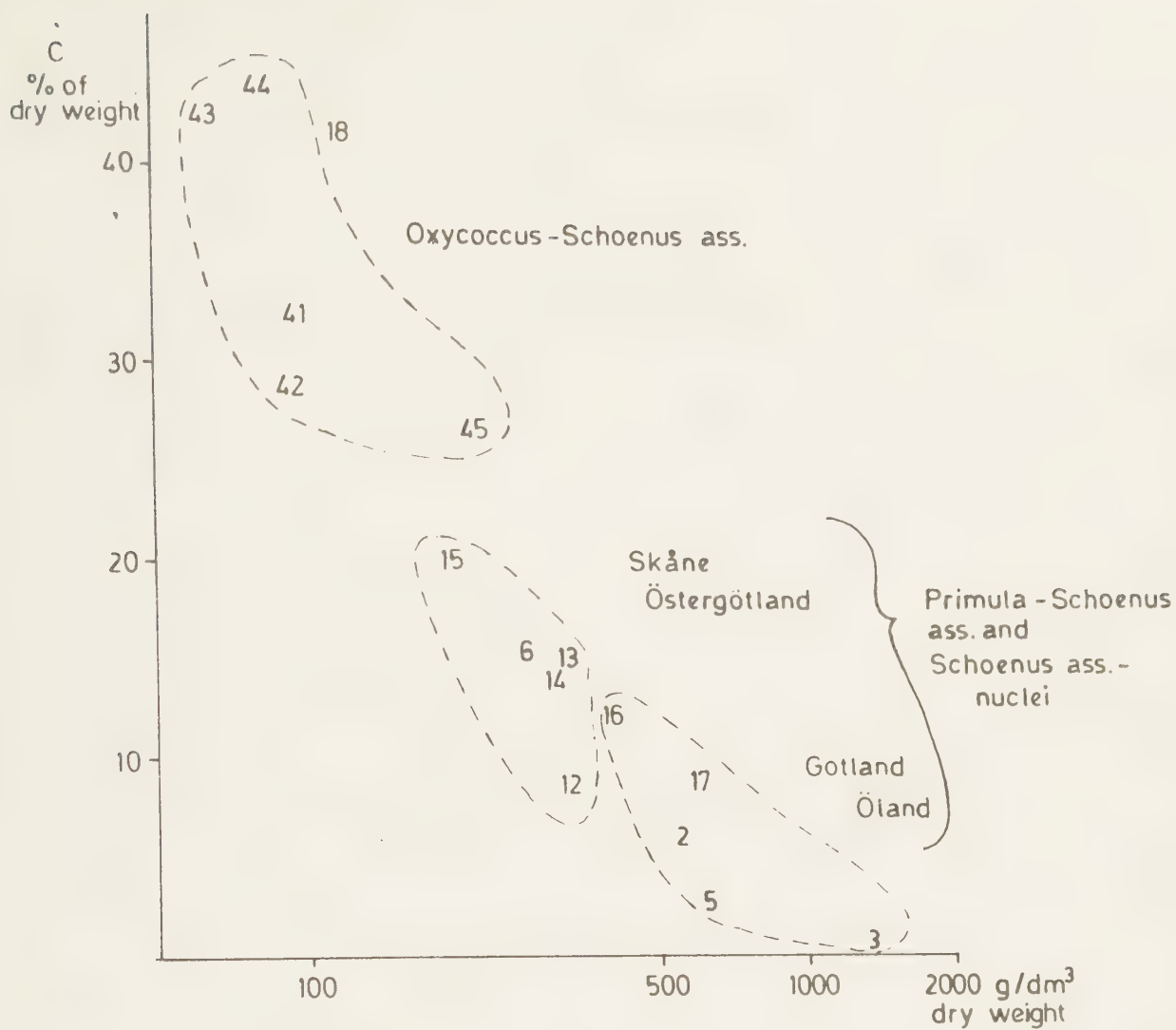


Fig. 12. Distribution of phytocoena in relation to the content of organic carbon and to dry weight.

Table 1. Scores of environmental variables on axes obtained by RA. Numbers 1 - 5, ordination of environmental variables, number 6, ordination of environmental variables and 136 selected species. Number of stands: ordination 1 - 4, 173; ordination 5, 176; ordination 6, 173.

	Eigenvalue	Tussock-height (Tus)	'Peat'-thickness (Pt)	pH	Dry weight (Dw)	Water content (Wt)	Carbonate (CO ₃)	Organic carbon (C)	Nitrogen (N)	C:N	Base saturation (Bs)	CEC	Calcium (Ca)	Ca:Mg	Phosphorous
Axis 1															
Ord. 1	.122	68	0	71	100	57	95	33	69	62	70	80	70	91	68
2	.128	69	0	71	100	57	95	33	69	62	70	80	70	91	-
3	.130	-	100	29	0	43	5	67	31	38	30	20	30	9	-
4	.070	-	-	54	100	34	96	0	52	40	53	70	54	92	34
5	.117	-	-	43	-	30	100	0	-	31	42	-	44	89	-
6	.128	-	75	39	23	46	26	59	40	44	39	34	39	28	41
Axis 2															
Ord. 1	.054	81	91	83	83	84	83	93	89	85	83	86	83	100	0
2	.039	49	59	35	0	43	100	43	62	30	35	52	38	75	-
3	.039	-	41	66	100	57	0	58	38	70	65	49	63	26	-
4	.055	-	-	75	60	81	60	100	80	81	75	72	75	78	0
5	.049	-	-	41	-	40	100	26	-	39	40	-	39	0	-
6	.047	-	30	32	34	31	30	27	28	31	32	30	32	25	49
Axis 3															
Ord. 1	.037	51	43	64	100	55	0	56	36	68	63	47	61	28	39
2	.033	63	0	59	4	77	32	100	73	70	60	49	59	27	-
3	.034	-	100	41	96	23	68	0	27	30	41	51	41	73	-
4	.038	-	-	59	100	48	0	46	30	62	58	44	56	28	37
5	.025	-	-	0	-	43	52	100	-	20	2	-	5	36	-
6	.043	-	90	86	81	87	96	86	90	85	86	89	87	91	92
Axis 4															
Ord. 1	.023	35	100	41	95	23	67	0	27	29	40	49	40	71	25
2	.022	33	26	38	17	41	100	23	11	45	38	26	37	0	-
3	.023	-	74	61	83	58	0	76	88	55	62	74	63	100	-
4	.022	-	-	43	7	54	100	41	0	61	43	25	43	30	21
5	.003	-	-	42	-	100	50	0	-	47	48	-	53	58	-
6	.035	-	52	43	51	40	45	38	42	41	43	44	43	46	42

Table 2. Soil properties of phytocoena. Arithmetic means and standard deviations are given. Only in a few cases the mean and the median value differs considerably.

Phytocoenon	Phytocoenon no	Number of samples	Height of tussocks (cm)	'Peat'-thickness (cm)	Dry weight	Water content	Organic carbon (C)	Nitrogen (N)	C:N	pH	Carbonate (CO ₃)	Base saturation	CEC	Ca saturation	Ca:Mg	Phosphorous (P)	Soil 2
<i>Oxyccus-Schoenus ferrugineus</i> ass.	44	3	9 (3)	35 (5)	83 (14)	90 (1)	43 (1)	166 (48)	19 (2)	6.2 (0.2)	<1	80 (6)	93 (6)	75 (6)	22 (6)	5 (2)	fen peat
<i>Utricularia-Drepanocladus badius</i>	43	6	9 (3)	77 (59)	62 (13)	92 (1)	42 (3)	104 (24)	22 (2)	6.5 (0.3)	<1	86 (6)	77 (21)	82 (7)	31 (10)	16 (13)	-
<i>Utricularia-Drepanocladus revolvens</i>	42	3	12 (2)	35 (9)	92 (16)	89 (2)	39 (2)	131 (28)	23 (1)	7.0 (0.2)	<1	89 (9)	120 (6)	83 (8)	20 (2)	12 (11)	-
<i>Riccardia sinuata-Mertensia hibernica</i>	41	12	16 (7)	117 (76)	96 (21)	90 (2)	43 (2)	183 (70)	20 (6)	6.5 (0.4)	<1	90 (5)	118 (22)	85 (5)	27 (7)	13 (6)	-
<i>Selaginella-Pinus</i>	45	6	10 (7)	86 (91)	215 (143)	76 (12)	27 (16)	267 (98)	14 (1)	7.1 (0.8)	12 (19)	98 (4)	178 (35)	93 (3)	34 (17)	43 (54)	muck
<i>Sesleria-Carex hostiana</i>	5	3	4 (4)	1 (2)	613 (158)	44 (13)	3 (2)	101 (25)	13 (1)	7.8 (0.2)	32 (43)	98 (3)	172 (92)	91 (9)	39 (45)	126 (134)	marl, clay
<i>Cladonia-Schoenus nigricans</i>	7	2	7 - 17	0	1310 (80)	25 (2)	<1	48 (6)	13 (5)	7.6 - 7.7	1 - 11	100	99 (77)	67 - 81	2 - 5	16 (4)	sand, clay
<i>Glaux-Schoenus nigricans</i>	3	3	3 (0)	0	551 (154)	49 (8)	6 (3)	156 (28)	16 (3)	7.8 (0.2)	49 (36)	100 (0)	211 (17)	81 (7)	8 (4)	25 (3)	-
<i>Schoenus intermedius-Schoenus ferrugineus</i>	2	5	13 (9)	0										95 (4)	44 (32)		-
<i>Primula-Schoenus ferrugineus</i> ass.	18	3	15 (7)	50 (30)	117 (6)	85 (1)	42 (5)	248 (4)	16 (2)	6.3 (0.2)	<1	92 (7)	127 (21)	88 (7)	38 (18)	24 (7)	fen peat
<i>Myrica</i> (<i>Sesleria</i> group)	17	33	16 (7)	19 (31)	585 (363)	55 (19)	9 (6)	230 (96)	14 (2)	7.6 (0.3)	34 (26)	100 (2)	271 (54)	98 (2)	130 (58)	30 (18)	muck, clay
<i>Carex hostiana</i> - - -	16	24	13 (4)	10 (41)	387 (203)	62 (14)	12 (9)	220 (90)	15 (3)	7.7 (0.3)	54 (26)	100 (2)	211 (35)	96 (5)	47 (37)	44 (40)	-
<i>Tortifolia</i> - - -	15	9	13 (6)	87 (92)	181 (90)	86 (7)	20 (11)	179 (79)	17 (3)	7.1 (0.2)	35 (30)	100 (0)	157 (30)	96 (2)	53 (36)	52 (23)	-
<i>Carex lepidocarpa</i> (<i>Bartsia-Ophrys</i> group)	14	16	20 (9)	42 (60)	311 (102)	71 (7)	15 (8)	228 (72)	15 (2)	7.2 (0.2)	48 (23)	100 (0)	191 (27)	97 (2)	81 (27)	35 (16)	-
<i>Calliergonella</i> - - -	13	11	19 (9)	47 (50)	324 (154)	73 (12)	16 (10)	198 (56)	16 (2)	7.0 (0.1)	37 (22)	99 (7)	218 (52)	96 (3)	51 (16)	60 (34)	-
<i>Carex lepidocarpa</i> (<i>Valeriana</i> group)	12	10	14 (7)	32 (24)	321 (155)	70 (15)	9 (6)	134 (63)	14 (2)	7.0 (0.1)	1 (1)	100 (0)	145 (51)	95 (2)	36 (18)	68 (44)	-
<i>Calliergonella</i> - - -	6	3	38 (8)	37 (12)	266 (108)	74 (9)	16 (15)	186 (91)	13 (4)	7.0 (0.1)	28 (46)	100 (1)	180 (47)	96 (11)	40 (15)	103 (59)	-
<i>Fissidens oerandoides-Schoenus nigricans</i>																	

Compound calculations: Dry weight, g dried soil/dm³ intact soil; water content, percent of fresh weight; CO₃, CaCO₃ in percent of dry weight; C, percent of dry weight; nitrogen, mmol/dm³ intact soil; CEC, sum of me cations/dm³ intact soil; base saturation, metal ions in percent of CEC; Ca, in percent of CEC; phosphorous, μmol P /dm³ intact soil.

1) In these means n equals to 7 (43), 8 (5), 13 (13), 12 (12). Phytocoenon numbers in brackets.

+) pH measured in water suspension.

2) Roughly estimated in the field and laboratory.

Table 3. Relationships between phytocoena and soil water
Compare also Fig. 3 in Tyler (1979 a).

A. Topogeneous soil water

1. Constantly high water table
Oxycoccus-Schoenus ferrugineus ass.
2. Temporarily flooded
Tofieldia and Carex hostiana phytocoenon of
the Primula-Schoenus ferrugineus ass.
Glaux phytocoena
Cladium-Schoenus nigricans phytocoenon
Schoenus intermedius-Schoenus ferrugineus
phytocoenon

B. Soligeneous soil water

1. Constantly high water table
Bartsia-Ophrys and Valeriana groups of
the Primula-Schoenus ferrugineus ass.
Fissidens-Schoenus nigricans phytocoenon
2. Temporarily flooded
Sesleria group of the Primula-Schoenus
ferrugineus ass.

SOIL ACIDITY AND DISTRIBUTION OF SPECIES ON TUSSOCKS
AND INTERSPACES IN SCHOENUS VEGETATION OF SOUTH AND
SOUTHEAST SWEDEN

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Keywords:

Bryophyte sequence, Linear regression, pH, Reciprocal averaging, Schoenus, Sphagnum, Sweden, Vertical distribution.

⁺ Nomenclature as in Tyler 1979 a)

⁺⁺ The study is the third part of a doctor's thesis.

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INTRODUCTION

An area with a *Schoenus* phytocoenosis (cf. Tyler 1979 a) is rarely quite smooth. The development of tussocks seems to be independant of grazing in contrast to many other fen phytocoenoses (Pigott 1956, Pettersson 1958). The tussocky appearance of these phytocoenoses may be due to a combination of growth form of the *Schoenus* species and fluctuations of the water table. The *Schoenus* stems and roots are able to collect and hold together the soil (peat or muck) during times of flooding while the soil in the lower interspaces is washed away. Several investigators have observed the differences in species composition between tussocks and interspaces (Booberg 1930, Sjörs 1948, Ruuhijärvi 1960, Larsson 1967, Moen 1970). Most authors state that *Scorpidium scorpidioides* and *Drepanocladus revolvens* are typical of the interspaces and *Campylium stellatum* of the tussocks, though *Drepanocladus* is sometimes replaced by *Campylium* also in the interspaces. With reference to Du Rietz (1949) Larsson (op.cit.) relates the dominance sequence *Scorpidium* - *Drepanocladus* - *Campylium* to a moisture gradient. Du Rietz regarded the sequence as a feature typical of all rich fens and representing a successional development. Two more species, *Tomenthypnum nitens* and *Sphagnum fuscum*, were added to the sequence, representing final stages. The corresponding differentiation of the field layer was discussed by Booberg (op.cit.), Malmer (1965), Kask (1965) and Larsson (op.cit.). Booberg, Kask and Larsson published descriptive data illustrating the differentiation of the field and bottom layers. A similar differentiation of calcareous fen meadow phytocoena (cf. Tyler 1979 a) in *drepanocladetosum* and *ctenidietosum* was discussed and documented by Hallberg (1971). *Ctenidium molluscum* and *Fissidens adianthoides* are stated as species growing on the tussocks also by Larsson (op.cit.) and Malmer (op.cit.).

The variation in pH has been studied in many investigations of rich fens (Booberg 1930, Sjörs 1948, Witting 1947, 1948, Gorham 1956, Pigott 1956, Trass 1957, Havas 1961, Persson 1962, Moen 1969). Measurements have been made directly in the highly organic soils (peat or muck), in water suspensions, or in the mire (bog and fen) water. pH of mire water is always higher than pH measured directly in the corresponding peat (Gorham, op.cit.). The relation between pH, height above a reference level, and species composition of the phytocoenoses was studied by van der Maarel & Leertower (1967) in a dune slack with *Schoenus nigricans*. Inverse relationships between pH and height was demonstrated, while Booberg (1930) measured a higher pH at the top of the tussocks than in the interspaces.

The aim of the present paper is to discuss the vegetational gradient from tussocks to interspaces in the *Schoenus* phytocoenoses and to demonstrate if it is in accordance with the bryophyte sequence mentioned above, if also other species are unevenly distributed, and if the same zonation occurs in the whole investigation area. To study pH gradients and their relations to bryophyte zonations is another purpose.

METHODS

Field work

The field work was carried out in the summers 1972 and 1973 in Southeast Sweden (cf. Tyler 1979 a). In both years the precipitation during June - August was below average Gotland 1972 and Skåne 1973 had very little summer rain, only about one third of the means of 1931-1960 (SMHI 1972, 1973). Belt transects comprising tussocks and interspaces were described at twenty sites (for site position see Tyler 1979 b). A tape measure was fixed with hairpins on the surface in N-S direction. The transect was levelled by help of a steel stick, a ruler, and a bubble level. The soil surface

along the transect (length 1-2 m) was cut into quadratic squares, sides 3-10 cm, to a depth of about 3 cm. The vascular plants within the squares were noted and the pieces put into plastic bags and deep frozen.

Laboratory work

Immediately after thawing (in the bags) the whole sample was immersed into demineralized water. Amount of water was adjusted according to size and moisture of the sample. After three hours pH was measured electrometrically in the soil sample. The bryophyte species were determined microscopically and the quantitatively most important species was indicated.

Numerical analysis

Reciprocal averaging (RA, Hill 1973) was performed, in order to reveal species patterns and gradients within the transects. Unipolar axes are obtained if species of irregular occurrence are included (cf. Gauch et al. 1977). Therefore such species were omitted. The size of the material and the many species with restricted occurrences necessitated separate treatment of data from the different provinces. Successive squares of the size 3 x 3 cm were paired before analysis, i.e. those from Östergötland and Öland.

The squares were most often plotted according to their loadings on the first axis, or on any subsequent axis (x-axis) and the height above bottom of the transect (y-axis). A relation between moisture conditions and bryophyte species was assumed according to literature evidence. The same bryophyte species occurs on different height above the interspaces in different transects. Hence, for reasons of comparison, the transects had to be vertically dislocated. The distribution of species and squares in the ordination planes gives both the order between the transects and indicates the degree of dislocations because associated squares from different transects ought to be located at the same height level. However, the exact degree of dislocation is subjectively

decided, because a reciprocal adjustment of the transects are made, in order to obtain coincidence between the distribution of the most frequent bryophytes. Field notes on water levels have also been used.

The pH values were plotted against the height above the lowest point of the transects, but, in order to facilitate comparisons, the heights were transformed to height indices, x , using the formula:

$$x = 10 a : h \quad (1)$$

where a is the vertical distance from the lowest point of the transect and h is the distance between the highest and lowest points. The estimated regression coefficient of pH on the corresponding height index was calculated for each transect. If the relation between pH and height obviously was expressed as a curve, the transect was divided into parts. Significance levels of each regression coefficient was tested by a Student's t -test ($n < 30$) or a standard error test ($n > 30$). All calculations were made according to Bailey (1969).

RESULTS

Species composition of belt transects

Province of Uppland

In Uppland high Sphagnum hummocks are often found interspersed in the Schoenus phytocoenoses. The species composition of two hummocks are described in transects VII and IX (site nos. 47 and 54, Tyler 1979 b). Transects VIII and X (site nos. 51 and 55, op.cit.) represent ordinary Schoenus phytocoenoses.

Transect diagrams (not published) show a distinct zonation of the Sphagnum hummocks. However, the zonation within the Schoenus phytocoenoses is less obvious and it seemed

difficult to distinguish one common sequence of dominating bryophytes and to conclude anything about other types of zonation.

Four species groups were distinguished by the indirect gradient analysis and corresponding groups of squares confined to different levels of the transects (Figs. 1-5). The first axis represents the vertical gradient and the second axis separates squares and species occurring above the *Schoenus* level. The lower parts of the transects were treated separately in order to elucidate the bryophyte sequence there more clearly (Figs. 6 and 7).

A generalized picture of the zonation of bryophytes and vascular plants is obtained from these analyses (Table 1). Zones no. 3 (*Campylium stellatum*) and 6 (*Sphagnum fuscum*) meet in transect VII and no. 6 is differentiated into three parts. In the lower part *Schoenus ferrugineus*, *Cratoneuron commutatum*, *Bryum pseudotriquetrum* and, *Cinclidium stygium* occur, in the intermediate part *Schoenus ferrugineus*, *Carex panicea* and *Empetrum nigrum*, and in the highest part *Empetrum nigrum*, *Oxycoccus quadripetalus*, *Pinus sylvestris*, *Ledum palustre*, and *Rhamnus frangula*.

Provinces of Öland and Gotland

The only transect from Gotland (XI) extends over a spring flush in the Lojsta mire (site no 36, Tyler 1979 b). *Cratoneuron commutatum* and *Campylium stellatum* are growing from the water level to over the tussock but *Cratoneuron commutatum* has the highest cover at low levels. *Drepanocladus revolvens* occurs on the top.

The four transects from Öland (XII-XV) represent spring fens or the vicinity of recurrent pools (Sw. vät) (site nos. 20, 17, 22, 24, Tyler 1979 b).

A sequence of transects is obtained in the plane of axes 1 and 3 (Fig. 8). Both axes seem to represent moisture gradients: a wet-dry gradient and obviously also a gradient from mobile to stagnant water indicated by *Cratoneuron commutatum* and *Scorpidium scorpidioides* respectively. Transect XI is distinguished by the occurrence of *Cratoneuron commutatum* and is well separated from the other transects (Fig. 9). The dislocations are made in the way previously described. The bryophyte zonation (Fig. 9) is not distinct. A lower zone with *Cratoneuron commutatum* (dominant) and *Riccardia pinguis*, and a higher zone with *Cratoneuron commutatum* and *Drepanocladus revolvens* or *Campylium stellatum* as alternating dominants may perhaps be distinguished. The higher zone is also present in transect XV, where it is followed by a *Ctenidium molluscum* - *Fissidens adianthoides* zone. Also in the transects XII - XIV the zonation is indistinct (Fig. 10). Here *Ctenidium molluscum*, *Campylium elodes*, *Fissidens adianthoides* and *Ditrichum flexicaule* mainly occur above the level 14 cm and *Scorpidium scorpidioides* and *Drepanocladus revolvens* below that level. Only two of the vascular plants seem to avoid the lowest levels: *Potentilla erecta* and *Sesleria coerulea*. All other species shown in Figs. 11-12 have a fairly even distribution on interspaces and tussocks.

There is no doubt that the individual transects of Öland and Gotland are zonated but it is less easy to find a generally valid sequence of species (Table 2).

Province of Skåne

Transects XVI-XX (site nos. 8a, 8b, 6a, 6b, 7a, Tyler 1979 b) are all from SE Skåne as *Schoenus* wetlands are mainly confined to that part of the province. Transect XVII represents the *Fissidens osmundoides* - *Schoenus nigricans* phytocoenon poor in species (cf. Tyler 1979 a). Only two vascular plants and a few bryophytes occur in this transect on the tops and sides of the high tussocks. The *Schoenus*

phytocoenosis at Benestad (transects XIX, XX) covers the gently sloping top areas of tufa hills and are permanently flushed. No distinct zonation common to all transects can be discerned by direct inspection of the transect diagrams. The liverworts *Calypogeia fissa*, *Calypogeia mülleriana*, and *Cephalozia connivens* are growing on the top areas whereas all other bryophytes occur almost everywhere except on the tops of the highest tussocks.

Indirect gradient analysis does not separate the transects into distinct fields in the first ordination plane, as is the case in the materials from Uppland and Öland-Gotland (Fig. 13). The first axis is unipolar, also after exclusion of *Cephalozia* species and *Schoenus nigricans*. These species made the first axis even more distinctly unipolar. The assumed moisture gradient represented by the bryophyte sequence *Cratoneuron commutatum* - *Drepanocladus revolvens* - *Campylium stellatum* - *Ctenidium molluscum* is obtained on the second axis. This sequence is complemented by *Calypogeia* species on the first axis. However, *Ctenidium molluscum* occurs on all levels in the transects, also below the water level, and *Cratoneuron commutatum* and *Drepanocladus revolvens* are widely distributed, too, though not on the highest levels (Fig. 14). The only bryophytes with limited distribution are *Cephalozia* and *Calypogeia* species, *Preissia quadrata* and *Riccardia pinguis* (Fig. 15, 16). Shoots of *Schoenus ferrugineus* occur on all levels, of *Schoenus nigricans* on the highest tops only. To a certain degree other vascular plants have a restricted vertical distribution (Fig. 17, 18 Table 3).

Province of Östergötland

Most transects from Östergötland (site nos. 37, 38, 39, 40, 41, 46a, Tyler 1979 b) are from the largest *Schoenus* wetlands in that province. Differences between tussocks and interspaces occur in some of these transects but no generally valid zonation can be distinguished by direct inspection of

the transect diagrams. Transect VI is laid over a small rill. As in Skåne, *Ctenidium molluscum* is growing below the water level and no distinct zonation appears.

The distribution of species on different levels is difficult to survey. Each transect is in fact unique. In spite of several ordination attempts no easy interpretable gradients were obtained (Figs. 19-23). Only in two cases (Figs. 20 and 21) the distribution of species might be interpreted as a gradient: stagnant water - mobile water - drier conditions, diagonally from the lower right to the upper left corner of the ordinations planes. The zones with occurrences of *Ctenidium molluscum*, *Ditrichum flexicaule*, and *Preissia quadrata*, and the zone with *Cratoneuron commutatum* and *Drepanocladus revolvens* are very wide when squares of all transects are plotted against height in the same diagram (Fig. 24). The dislocations in this diagram are based on field notes and the sequence of the transects in Fig. 19. However, no axes obtained by ordination of the transects from Östergötland are possible to use for such diagrams, due to numerals of species with restricted occurrences.

The species distributions in each transect are obtainable from the ordinations (Figs. 25-28). Transect I lacks all vertical differentiation and is not illustrated, while transect IV is distinctly divided into a top and a bottom level, though without differences between the northern and the southern tussock slopes (Fig. 25). Such differences are obvious in transects II, III, V and VI (Figs. 26-28). In three of these transects *Drepanocladus revolvens* occurs on the north slopes and in the bottom of the interspaces, *Bryum pseudotriquetrum* on the south slopes. However, similarity in other species distributions is lacking.

Soil pH and bryophyte sequence

The pH value of each sample was indicated in the transect diagrams. The curves connecting the dots often seemed to

form an inverse picture of the height curve of the transects but sometimes the dispersion was too large to allow the distinction of a pattern.

Four types of relations between heights and pH values are found (Fig. 29, Table 4). In some cases the pH values do not differ distinctly between tussocks and interspaces though the relations are mostly significant. In other cases the relations are inverse and linear. However, in most transects the regression is curvilinear with the highest pH at some distance above the lowest point. In two transects, finally, two distinct groups of pH values occur. There is no general relationship between pH amplitude and height of the transects. The pH differences per unit (cm) height is below 0.10. Only transects I, III, and VIII exhibit higher values. The pH amplitude is varying, very wide (pH 3.8 - 7.6) in two transects of Uppland but narrow in all transects from Skåne.

The relationships between soil pH and bryophyte sequences are in accordance with the four types mentioned. Mostly when the pH - height relation is linear (the two first mentioned types) *Ctenidium molluscum* is distributed on all levels (exceptions are transects IV and XIV, Table 4), but is never dominating (except in transect VI). Other bryophytes may either have a similar scattered distribution (transects I, XIX and XX) or be distinctly dominating on one particular level (transect XVI). In transects IV and XIV there are distinct dissimilarities between tussocks and interspaces and in transect II the three groups of pH values correspond to one particular group of bryophytes, though *Ctenidium molluscum* and *Fissidens adianthoides* are growing on all levels (cf. Fig. 26).

Distinct differences in species composition and dominance between the height levels occur in all transects where the pH - height relation is curvilinear or the pH values are separated into two groups (Table 4). Only in two transects

(XVII and XVIII) *Ctenidium molluscum*, *Campylium stellatum* and *Drepanocladus revolvens* occur on all levels but in these transects other bryophytes have a zonated distribution. The change in species composition and bryophyte dominance are sometimes very sharp and the level almost exactly corresponds to the level of the change in direction of the regression line (transects III, VII, VIII, IX, X, XII, XV, and XVII). The conformity is a little less perfect, though still distinct, in other transects (V, XI, XVIII). In the lower parts of all transects with curvilinear regression line *Scorpidium scorpidioides*, *Drepanocladus revolvens*, *Cratoneuron commutatum* or *Campylium stellatum* are dominating. In the higher parts of these transects *Campylium stellatum*, *Campylium elodes*, *Ditrichum flexicaule*, *Ctenidium molluscum*, *Bryum pseudotriquetrum*, *Preissia quadrata*, *Sphagnum rubellum* or *Sphagnum fuscum* are dominants.

DISCUSSION

No doubt, all individual transects of Uppland and Öland, some of Östergötland and Skåne are zonated, at least as far as some bryophytes are concerned. Further, similar zonations occur in transects from Uppland and Öland. Two types of bryophyte zonations (dominance sequences) are discussed in the literature: The *Scorpidium* - *Drepanocladus* - *Campylium* - *Tomenthypnum* - *Sphagnum fuscum* sequence (Du Rietz 1949) and the *Scorpidium* - *Drepanocladus*/*Campylium* - *Ctenidium* sequence (Pigot 1956, Malmer 1965, Larsson 1967, Hallberg 1971). The first sequence coincides mainly with the sequence found in Uppland, but the *Tomenthypnum* level is replaced by a *Sphagnum rubellum* level in the present material. The association proposed by Du Rietz (op.cit) between the dominance sequence and the water levels is already supported by Lumiala (1944) who demonstrated the decreasing hydrophily of the bryophytes discussed. Du Rietz considered the

Sphagnum hummocks to belong to the fen vegetation because *Carex* species occur on the tops and slopes. Other authors, however, regard the *Sphagnum* hummocks as a separate type of vegetation, a stage in a successional development towards a bog vegetation and indicating a meiotrophication (Ingmar 1963, Björkbäck 1965). The diverging zonation of the present transect VII corresponds to the 'transgression' of *Sphagnum fuscum* over *Schoenus* tussocks exemplified by Booberg (1930: 129).

The latter one of the bryophyte sequences above is the same as the sequence recorded from Öland in this study, especially if the position of *Campylium elodes*, *Preissia quadrata* and *Fissidens adianthoides* is considered (Malmer op. cit.). However, neither the results from Skåne nor those from Östergötland are comparable to the sequence mentioned. The occurrences in Östergötland of *Drepanocladus revolvens* and *Bryum pseudotriquetrum* on north and south slopes respectively only suggest some similarity to a sequence. In Skåne no general dominance sequence has been shown.

The lack of a zonation, common to all transects in each Skåne and Östergötland, may have different causes. The dislocation of the transects is a subjective treatment open to criticism. However, measurements of the incidental water level would have been of little use, because of the seasonal fluctuations (Lumiala 1944). The size of the sampling squares influences the number of species per square and the percentage of cover of the species. On the other hand the size of the squares is limited by the size and cylindrical form of the tussocks making it difficult to use transects broader than 6 cm. The size 3 x 3 cm was chosen since the first intention was also to study an assumed variation according to N-S exposure. A comparison of the results from the two provinces, where such small squares were used, show that a dominance sequence is obvious on

Öland but not in Östergötland. The total number of bryophytes in the transects from Östergötland is twice that number from Öland but the size of the squares should not have influenced the result from Östergötland. Determining factor is the unique species composition of each transect from the latter province.

Both the bryophyte sequences in Uppland and Öland and the species compositions of some transects in Skåne and Östergötland are comparable with the developmental phases of the succession of small pools in the Netherlands where *Caricetum diandrae* is considered an optimum (Segal 1968). The six developmental phases mentioned by Segal, by him seen also in other calcareous fens in Europe, are closely related to the bryophyte sequences in Uppland, while only two of the first phases correspond to the sequences on Öland and Gotland. Some transects of Östergötland may be related to the phases under discussion in spite of the differences between sloping spring fens and pools. Thus, the initial *Equisetum fluviatile* phase is represented by transect III and the *Acrocladium* (*Calliergonella*) phase by transects II and IV. Further, the presence of *Cephalozia* and *Calypogeia* species on the high tussocks of *Schoenus nigricans* and *Schoenus ferrugineus* in Scania relates these phytocoenoses to the *Sphagnum amblyphyllum* phase though no *Sphagnum* occurs. However, the occurrences of *Ctenidium molluscum* on all levels, even below the water table, and the mixed occurrences of *Cratoneuron commutatum* or *Drepanocladus revolvens* and *Ctenidium molluscum* still remain to explain.

The main difference between the site conditions of the *Schoenus* phytocoenoses on Öland, and Skåne and Östergötland seems to be the different seasonal fluctuations of the water table. The soil water on Öland seems to ooze from very superficial sources which dry up in the summer months, while the seasonal fluctuations in the sloping fens of Skåne and Östergötland are small. The combination of a high soligeneous soil water table (cf. Tyler 1979 c), slopes and mucky soils may produce a sloping water table. The

properties of the mucky soils, the inhomogeneous mixture of mineral particles, tufa, muck and little decomposed *Schoenus* stems and leaves, result in a different water permeability. These conditions in combination with the sudden changes in air volumes between moist and fairly dry muck (Göttlich 1965), may give rise to suitable conditions for *Ctenidium molluscum* and e.g., *Drepanocladus revolvens* on the same height level in a particular transect.

Differences in bryophyte distribution between the north and south sloping sides of the tussocks may be predictable, because the relationships between certain bryophytes and certain moisture conditions seemed to be proved. A higher evaporation from the southern sides may result in the presence of *Ctenidium molluscum* and *Fissidens adianthoides* closer to the bottom of the interspaces on this side. *Scorpidium scorpidioides*, *Drepanocladus revolvens* and *Cratoneuron commutatum* could be expected to extend over parts of the northern sides. However, in only 8 out of 20 transects are there certain differences between the north and south slopes of the tussocks. The only common difference is the presence of *Drepanocladus revolvens* and *Scorpidium scorpidioides* higher above the bottom of the interspaces on the north slopes. In three transects from Öland *Fissidens adianthoides* and *Bryum pseudotriquetrum* occur only on the northward slopes near the top of the tussocks while *Ditrichum flexicaule* occurs on the high parts of the southward slopes. In Östergötland, however, *Bryum pseudotriquetrum* seems to prefer southward slopes.

In all provinces *Potentilla erecta*, *Cephalozia* species, *Calypogeia* species and *Ditrichum flexicaule* are always confined to the top of the tussocks. These top species are accompanied by *Schoenus* species, *Molinia coerulea*, *Sesleria coerulea*, *Primula farinosa*, *Parnassia palustris*, *Epipactis palustris*, *Riccardia sinuata*, and *Fissidens adianthoides*. In the interspaces *Cratoneuron commutatum* and *Riccardia pinguis* often occur together with *Juncus*, *Eriophorum* and *Carex* species. The intermediate levels are often occupied by an unordered

mixture of many species. *Campylium elodes* and *Preissia quadrata* mainly occur at these levels. *Schoenus ferrugineus*, *Molinia coerulea*, *Carex* species, *Bryum pseudotriquetrum*, and *Campylium stellatum* are often met with on all levels.

The similarity between the present result and the results of earlier studies (Booberg 1930, Pigot 1956, Havas 1961, Björkback 1965, Kask 1965, Malmer 1965, Larsson 1967, van der Maarel & Leertower 1967, Hallberg 1971) is greater in vascular plants than in bryophytes. Besides the species mentioned above *Selaginella selaginoides*, *Scirpus hudsonianus*, *Prunella vulgaris*, *Succisa pratensis*, and *Linum catharticum* are reported as tussock dwellers, while e.g. *Equisetum* species are mostly confined to the interspaces. Most *Carex* species grow both on tussocks and in interspaces both according to the present and earlier studies. However, *Carex dioica* is an exception. It is reported by several authors as a tussock dweller (e.g., Kotilainen 1927, Pigot op.cit., Björkback op.cit.) and is considered by Lumiala (1944) as very little hydrophilous. In my transects it is mostly found in the interspaces. Hallberg (op.cit.) has found it in both sites. The environmental demands of the species differs perhaps between northern and southern Fennoscandia.

As was accentuated by Havas (1961:103) the pH values given in the literature of 'peat' or water from rich fens are not comparable due to differences in methods of determination. Further the pH values of water are at least 0.5 pH units higher than those of corresponding 'peat' samples (Gorham 1956, Malmer 1962, Persson 1962). However, most pH values reported have a range of c.6 - c.8 (Witting 1947, 1948, Havas 1961, Sjörs 1961, 1971, Persson 1962). Fairly few measurements in *Schoenus* phytocoenoses are reported. The pH of soil water varies between 5.9 and 8.3 (Witting 1947, Sjörs 1948, Skogen 1965, Moen 1969) and the pH of 'peat' suspensions between 5.1 and 8.2 (Booberg 1930, Langer 1958, Eicke-Jenne 1960, Trass 1965). The total pH range of

the soil (peat or muck) from the *Schoenus* phytocoenoses of the present study is 5.2 - 8.2, thus in good agreement with literature recordings.

No pH differences between soil from tussocks and soil from interspaces in rich fen and calcareous wetland phytocoenoses are reported by Booberg (1930) Pankakoski (1935), Heikurainen (1953), and Hallberg (1971). However, van der Maarel & Leertower (1967) like the present author, found that pH decreases with the increase in height above the lowest point. Pankakoski (op.cit.) made the same observation as the present author, that the highest pH values often occur in the middle of the sides of tussocks and assumed that this was related to water fluctuations causing enrichment of lime at these levels by evaporation. The distinct difference in pH between *Schoenus* and *Sphagnum rubellum* or *Sphagnum fuscum* phytocoenoses is evidenced both in transects VII and IX (Fig. 29) and in Sjörs (1948:76), where almost the same species composition was recorded on higher levels. Most authors give pH <4.0 for *Sphagnum fuscum* peat (Kotilainen 1927, Sjörs 1948, Persson 1962, Sonesson 1970). In the present study pH is estimated to 3.7 - 4.4.

It may be assumed that the pH-equalizing effect of the water movements is one of the important factors influencing the pH-level of the soil along a transect over tussocks and interspaces. Then, the rather small differences in pH (≤1 unit) between top and bottom areas of some transects (cf. Fig. 29) may be the result of either a permanently high level of mobile water or of frequent and great fluctuations of the water level. Some of these transects in fact extend over small rills in spring fens. Inverse linear relationships between pH and height as well as much higher pH amplitude (>2 units of pH) may be demonstrated when the water movements are mainly capillary, and, the bottoms of the interspaces are seldom flooded. Only a few transects are of this type and they are sometimes distinctly zoned with

Calliergonella cuspidata at lower levels. Distinct curvilinear pH - height relations may be developed when the water level is close to the surface in the interspaces. Then the capillary water flow may reach a certain average level inside the tussocks and at this level the evaporation and the lime enrichment is the highest. The site conditions above and below that level are different in several respects. Most transects studied belong to this type (cf., Fig 29) and they mostly show a more or less distinct bryophyte zonation. Still more different site conditions occur when the calcareous soil water never reaches the higher parts of the tussocks which then may form an initial *Sphagnum* hummock. The great difference in pH between *Schoenus* tussocks with *Campylium stellatum* or *Drepanocladus revolvens* and with *Sphagnum rubellum* or *Sphagnum fuscum* may be due to both the different chemical properties of the litter and the deficiency of neutralizing soil water constituents (cf. Ingmar 1963).

SUMMARY

In five South Swedish provinces the vertical distribution of species in *Schoenus* phytocoenoses, especially bryophytes, were studied by belt transects and analysed by RA. Results indicate that the sequence of bryophyte dominants: *Scorpidium scorpidioides* - *Drepanocladus revolvens* - *Campylium stellatum* - *Tomenthypnum nitens* - *Sphagnum fuscum* reported by Du Rietz (1949) is distinctly developed in Uppland. A shorter sequence: *Scorpidium scorpidioides* - *Drepanocladus revolvens*/*Campylium stellatum* - *Ctenidium molluscum*, is developed on Öland. In Skåne and Östergötland it is not possible to demonstrate any bryophyte sequence common to all transects and probable reasons for this are discussed. The distribution of the vascular plants confirmed the results of earlier investigations. Several types of relationships between pH and height above interspaces are found and it is assumed that these relationships are due to water fluctuations.

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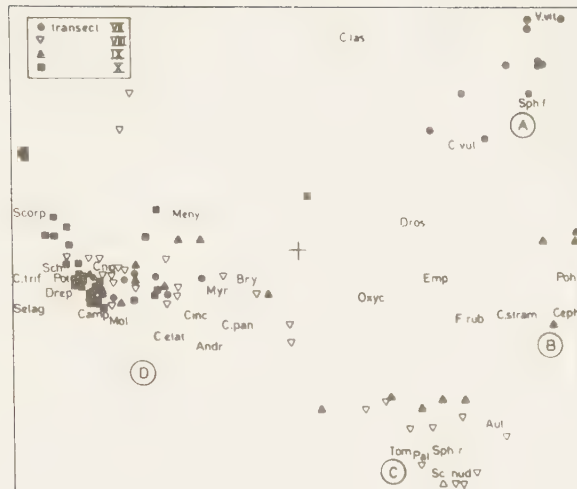


Fig. 1. Plot of species and squares on the plane of axes 1 and 2. Ordination of all transects from Uppland, 104 squares of size 10 x 10 cm, 37 species. Estimated eigenvalue: axis 1, 0.69; axis 2, 0.47. A. *Sphagnum fuscum* species group. B. *Pohlia sphagnicola* species group. C. *Sphagnum rubellum* species group. D. *Schoenus ferrugineus* species group.

Species represented in the figure: *Andromeda polifolia*, *Aulacomnium palustre*, *Bryum pseudotriquetrum*, *Campylium stellatum*, *Carex elata*, *Cephalozia connivens*, *Cinclidium stygium*, *Carex lasiocarpa*, *Carex nigra*, *Carex panicea*, *Calliergon trifarium*, *Calliergon stramineum*, *Calluna vulgaris*, *Drepanocladus revolvens*, *Drosera rotundifolia*, *Empetrum nigrum*, *Festuca rubra*, *Menyanthes trifoliata*, *Molinia coerulea*, *Myrica gale*, *Oxycoccus quadripetalus*, *Paludella squarrosa*, *Pohlia sphagnicola*, *Potentilla erecta*, *Scorpidium scorpidioides*, *Schoenus ferrugineus*, *Scirpus hudsonianus*, *Selaginella selaginoides*, *Sphagnum fuscum*, *Sphagnum rubellum*, *Tomenthyonum nitens*, *Vaccinium vitis idaea*.

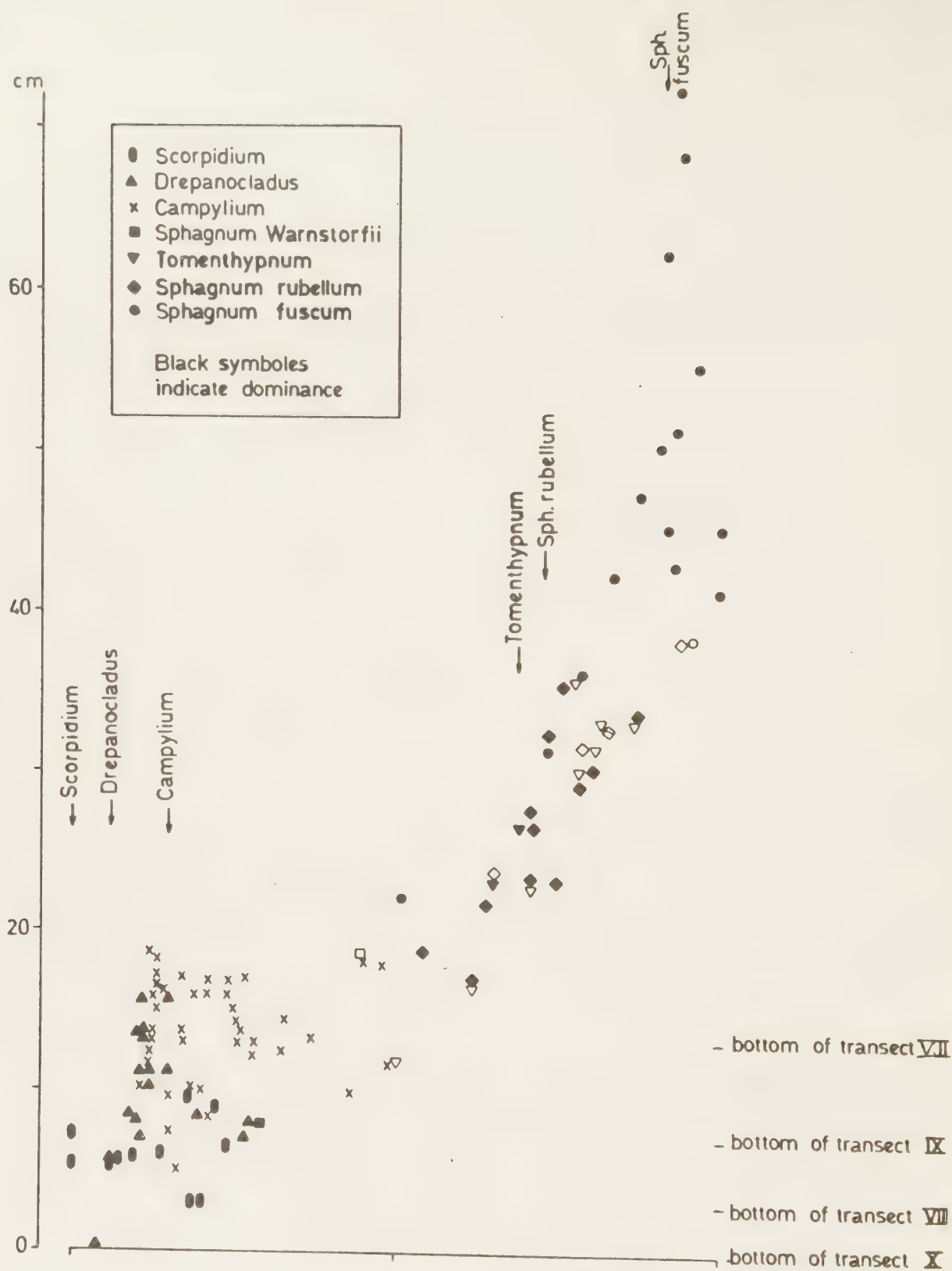


Fig. 2. Scatter diagram of squares with some bryophytes. X-axis is axis 1 of the same ordination as in Fig. 1, y-axis is the height from the bottom of the lowest interspace to the top of the highest hummock or tussock. The displacements of the bottom levels are described in the text. *Scirpidium scirpidioides*, *Drepanocladus revolvens* and *Campylium stellatum* are represented only where they are dominating. The arrows indicate species scores on the axis.

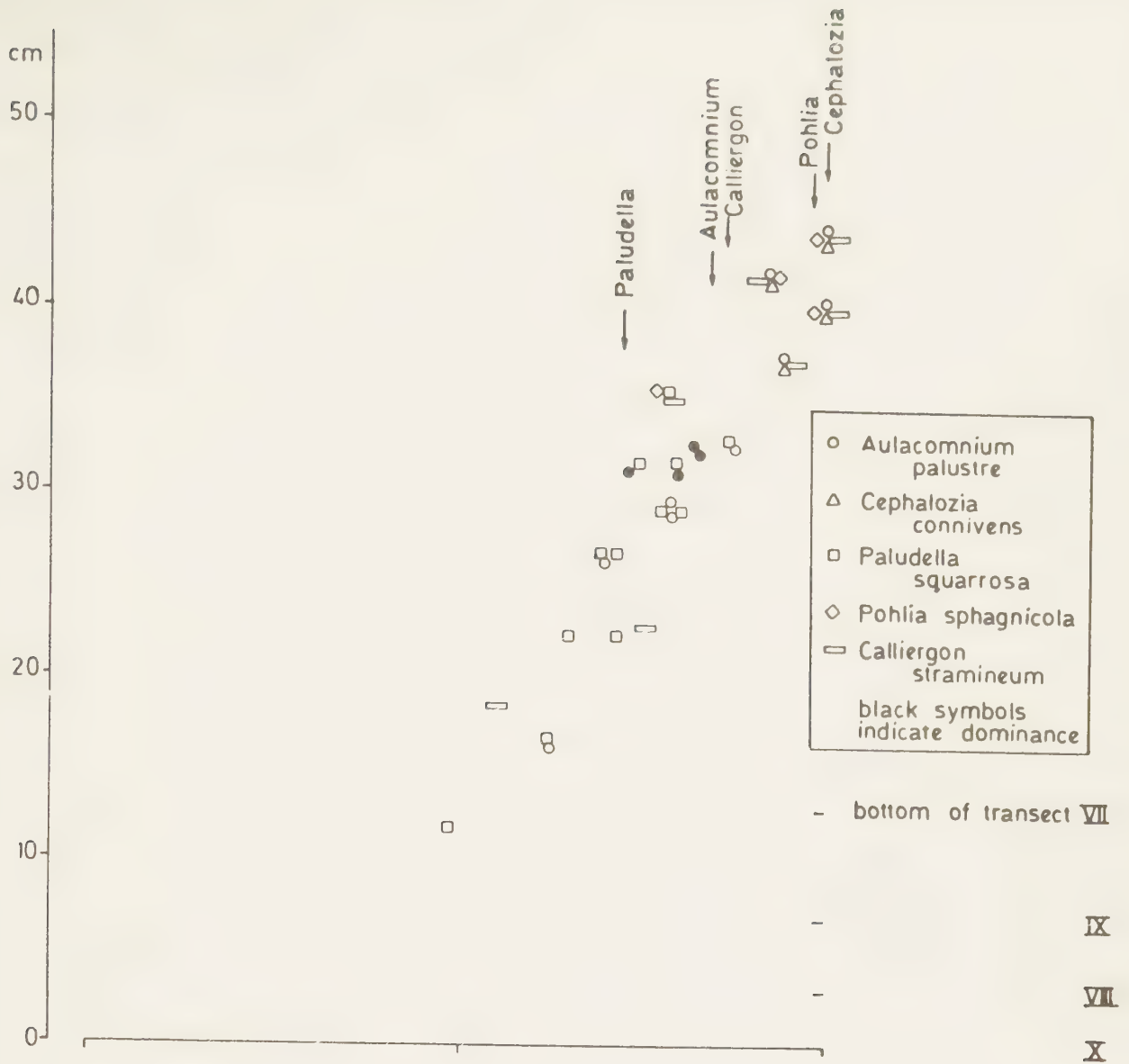


Fig. 3. Same as Fig. 2.

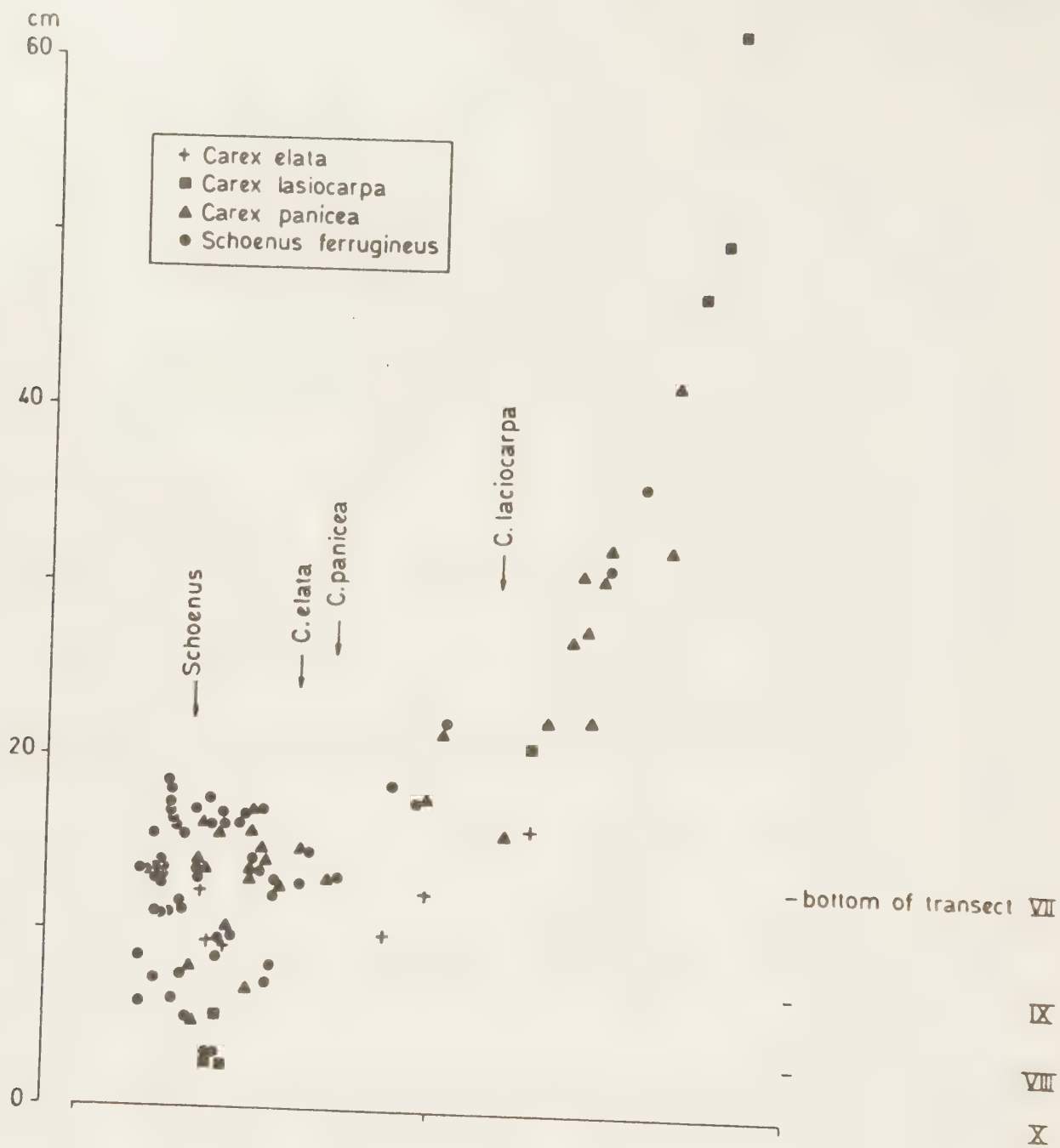


Fig. 4. Same as Fig. 2. Distribution of some vascular plants.

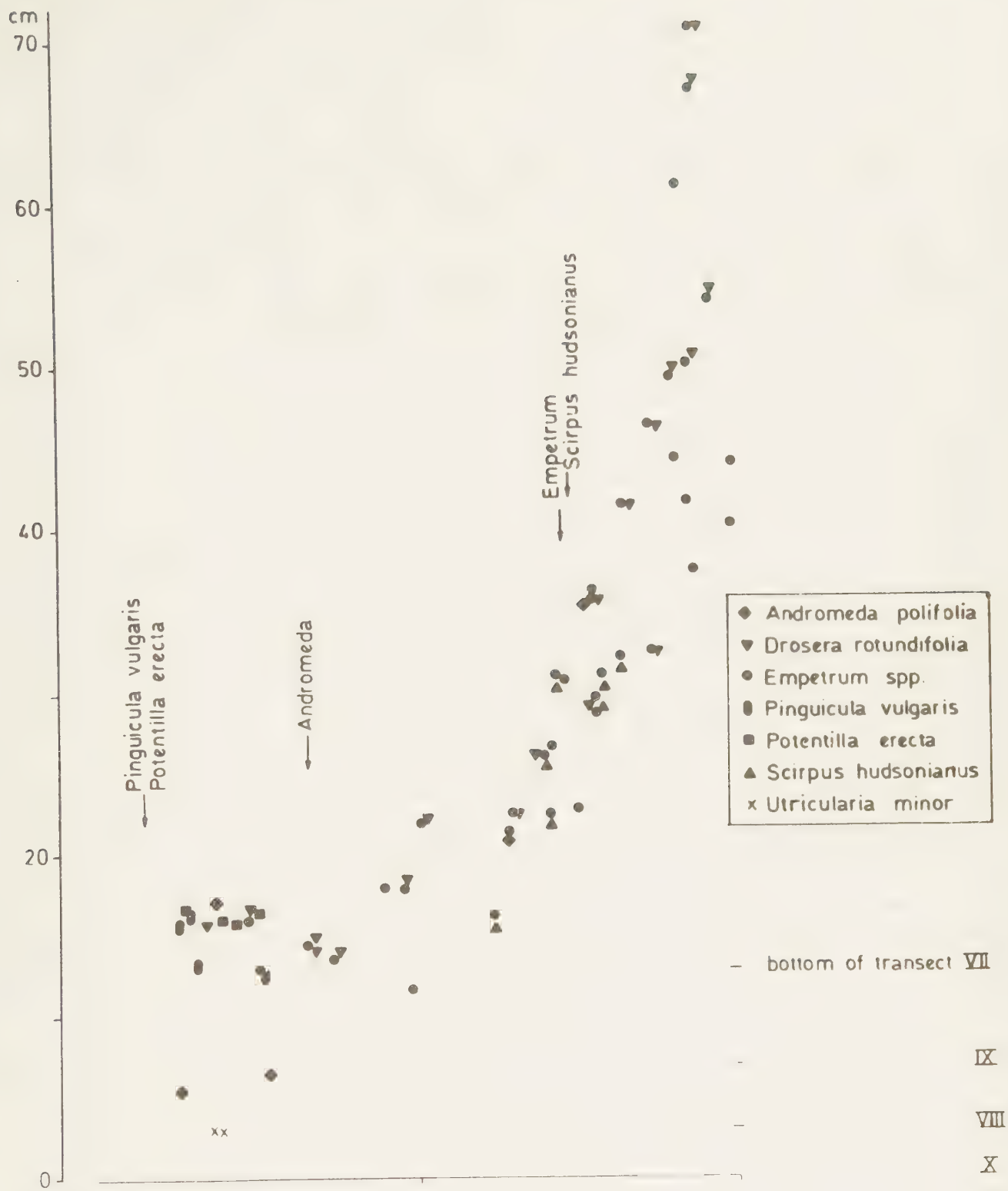


Fig. 5. Same as Fig. 4.

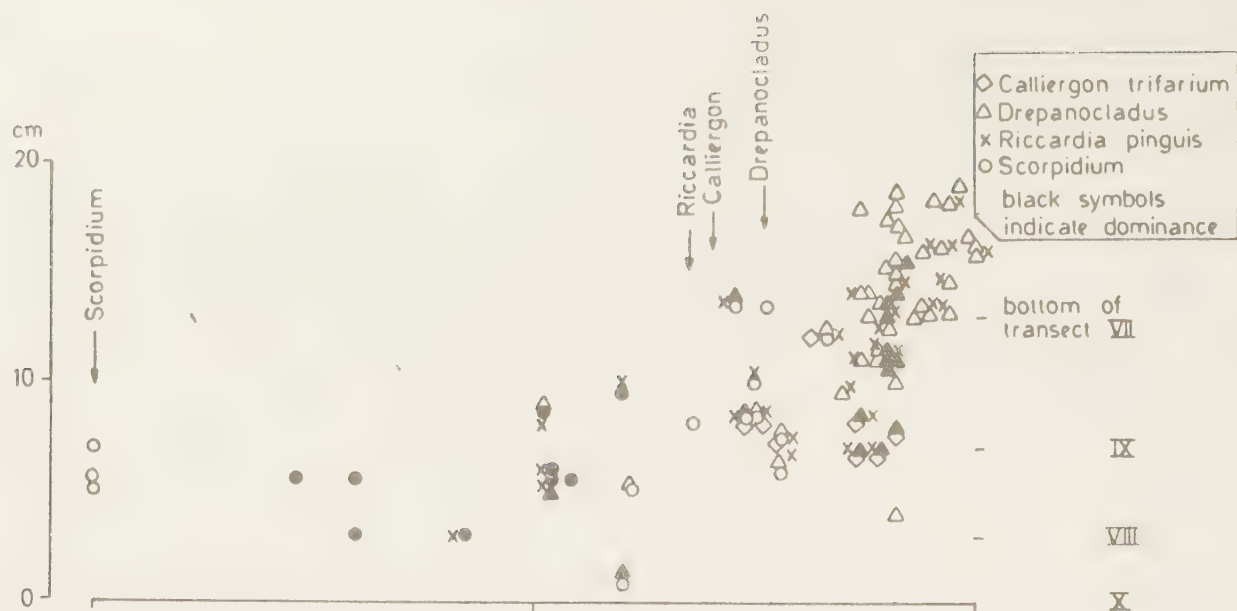


Fig. 6. Scatter diagram of squares with some bryophytes. X-axis is the first axis obtained by an ordination of the squares distributed in the lower parts of Fig. 2, 71 squares, 19 species.



Fig. 7. Distribution of *Campyllum stellatum* on the same squares as in Fig. 6. Black dots indicate dominance.

Table 1. Vertical zonation of interspaces, tussocks and hummocks in the *Schoenus* phytocoenoses of Upland. * indicates dominating bryophyte and ** alternative dominants. The zones are distributed in the transects in this way: zones 2 (3) and 6, transect VII; zones 1, 2 (3), and 4, transect VIII; zones 2, 3, 4, and 5, transect IX; and zones 1, 2, and 3, transect X. Mixed occurrence of the zones 2 and 3 is marked 2 (3). Height in cm.

ZONE	1	2	3	4	5	6
HEIGHT LEVEL	0 - 10	5 - 16	8 - 19	16 - 38	35 - 45	>45
BRYOPHYTES	<i>Scorpidium scorpidioides</i> * <i>Riccardia pinguis</i>	<i>Drepanocladus revolvens</i> * <i>Campylium stellatum</i> <i>Calliergon trifarium</i> <i>Riccardia pinguis</i>	<i>Campylium stellatum</i> * <i>Drepanocladus revolvens</i> <i>Sphagnum warnstorffii</i> ** <i>Paludella squarrosa</i> <i>Cinclidium stygium</i>	<i>Sphagnum rubellum</i> * <i>Tomentothamnium nitens</i> ** <i>Aulacomnium palustre</i> ** <i>Paludella squarrosa</i>	<i>Sphagnum fuscum</i> * <i>Aulacomnium palustre</i> <i>Pohlia sphagnicola</i> <i>Calliergon stramineum</i> <i>Cephalozia connivens</i>	<i>Sphagnum fuscum</i> *
VASCULAR PLANTS	<i>Schoenus ferrugineus</i> <i>Carex lasiocarpa</i> <i>Utricularia</i> species	<i>Schoenus ferrugineus</i> <i>Carex panicea</i> <i>Carex lasiocarpa</i> <i>Molinia coerulea</i> <i>Pinguicula vulgaris</i> <i>Andromeda polifolia</i>	<i>Schoenus ferrugineus</i> <i>Carex panicea</i> <i>Carex lasiocarpa</i> <i>Potentilla erecta</i> <i>Pinguicula vulgaris</i> <i>Andromeda polifolia</i> <i>Selaginella selaginoides</i> <i>Oxycoccus quadripetalus</i> <i>Empetrum nigrum</i> <i>Myrica gale</i>	<i>Schoenus ferrugineus</i> <i>Carex panicea</i> <i>Carex lasiocarpa</i> <i>Scirpus hudsonianus</i> <i>Andromeda polifolia</i> <i>Oxycoccus quadripetalus</i> <i>Empetrum nigrum</i> <i>Myrica gale</i>	<i>Carex lasiocarpa</i> <i>Oxycoccus quadripetalus</i> <i>Empetrum nigrum</i> <i>Myrica gale</i>	<i>Carex lasiocarpa</i> <i>Empetrum nigrum</i> <i>Vaccinium vitis idaea</i>



Fig. 8. Plot of species and squares on the plane of axes 1 and 3. Ordination of all transects from Öland and Gotland, 101 squares of size 3 x (2 x 3) cm, 21 species. Estimated eigenvalue: axis 1, 0.51; axis 3, 0.36.

Species represented in the figure: *Bryum pseudotriquetrum*, *Campylium stellatum*, *Campylium elodes*, *Carex dioica*, *Carex hostiana*, *Cratoneuron commutatum*, *Ctenidium molluscum*, *Ditrichum flexicaule*, *Drepanocladus revolvens*, *Drosera anglica*, *Fissidens adianthoides*, *Linum cathartica*, *Molinia coerulea*, *Potentilla erecta*, *Preissia quadrata*, *Primula farinosa*, *Riccardia pinguis*, *Schoenus ferrugineus*, *Scorpidium scorpidioides*, *Sesleria coerulea*.

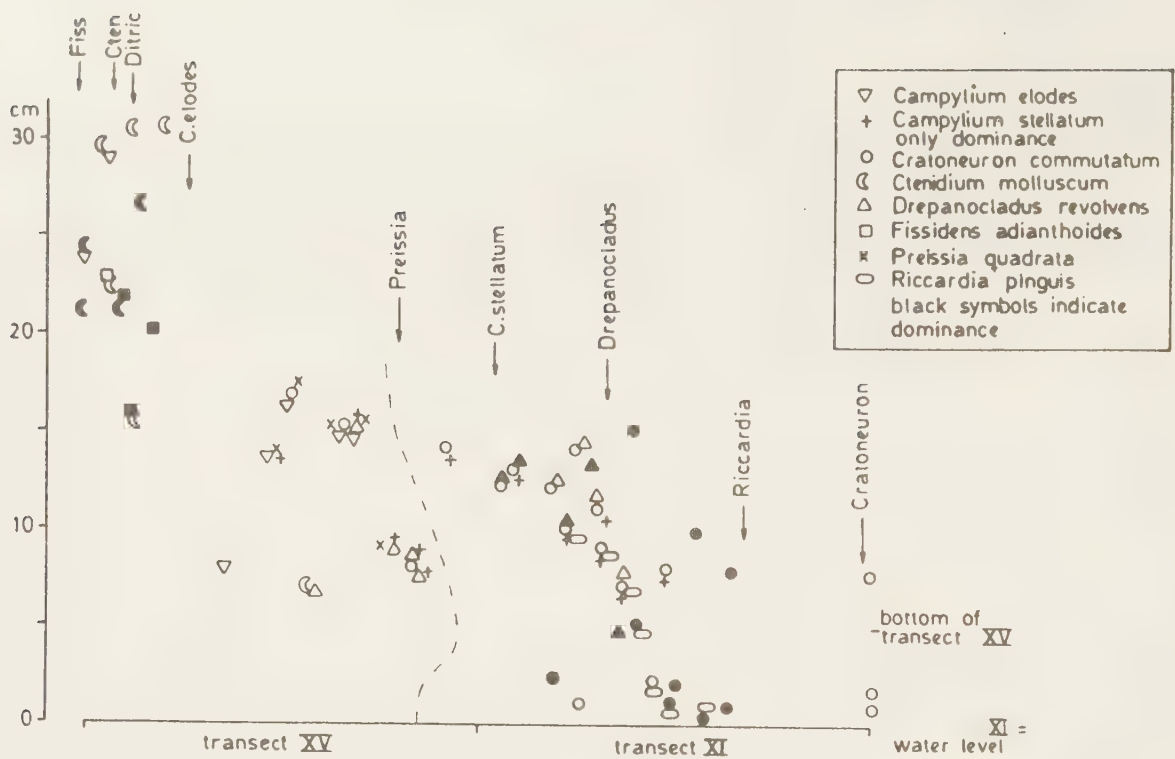


Fig. 9. Scatter diagram of squares with some bryophytes.

X-axis is axis 1 of the same ordination as in Fig. 8. The dashed line separates the squares belonging to each transect.



Fig. 10. Scatter diagram of some bryophytes. Axis and ordination as in Fig. 9.

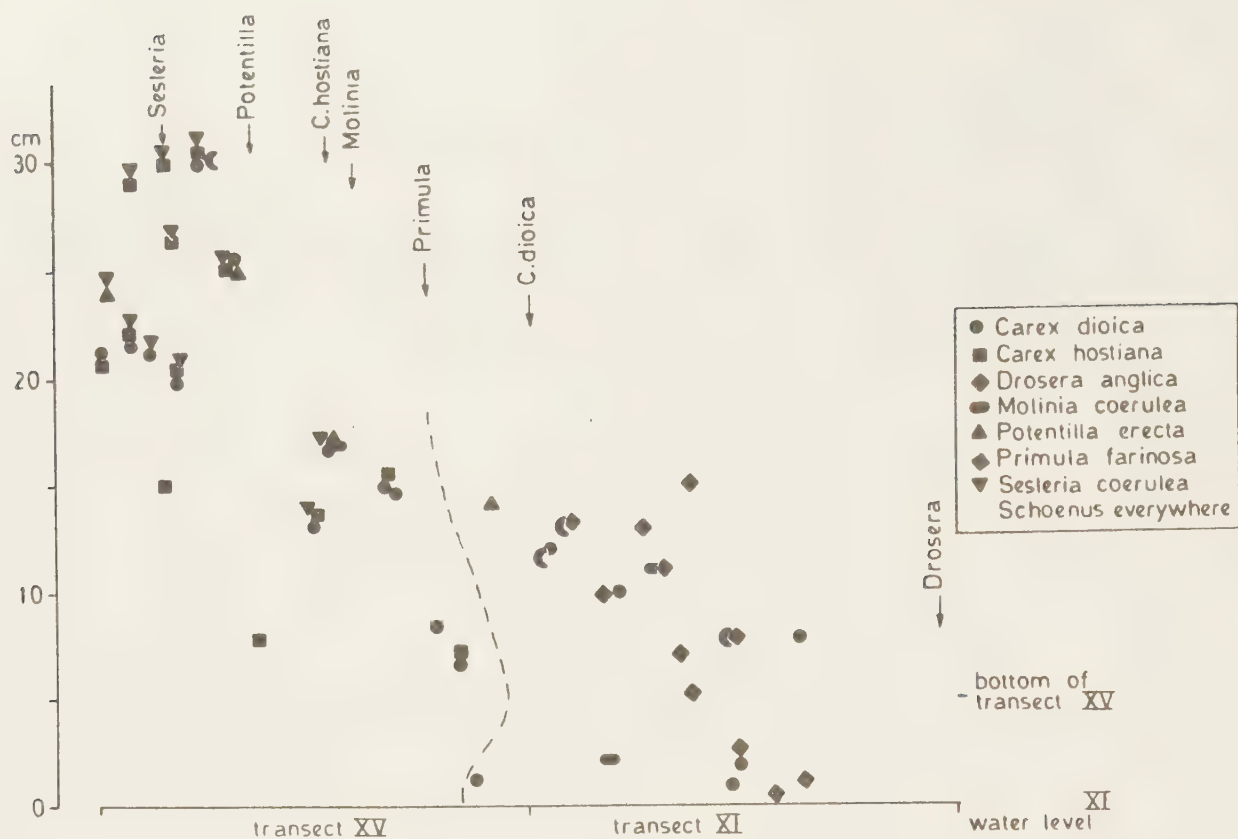


Fig. 11. Scatter diagram of squares with some vascular plants.
Axis and ordination as in Fig. 9.

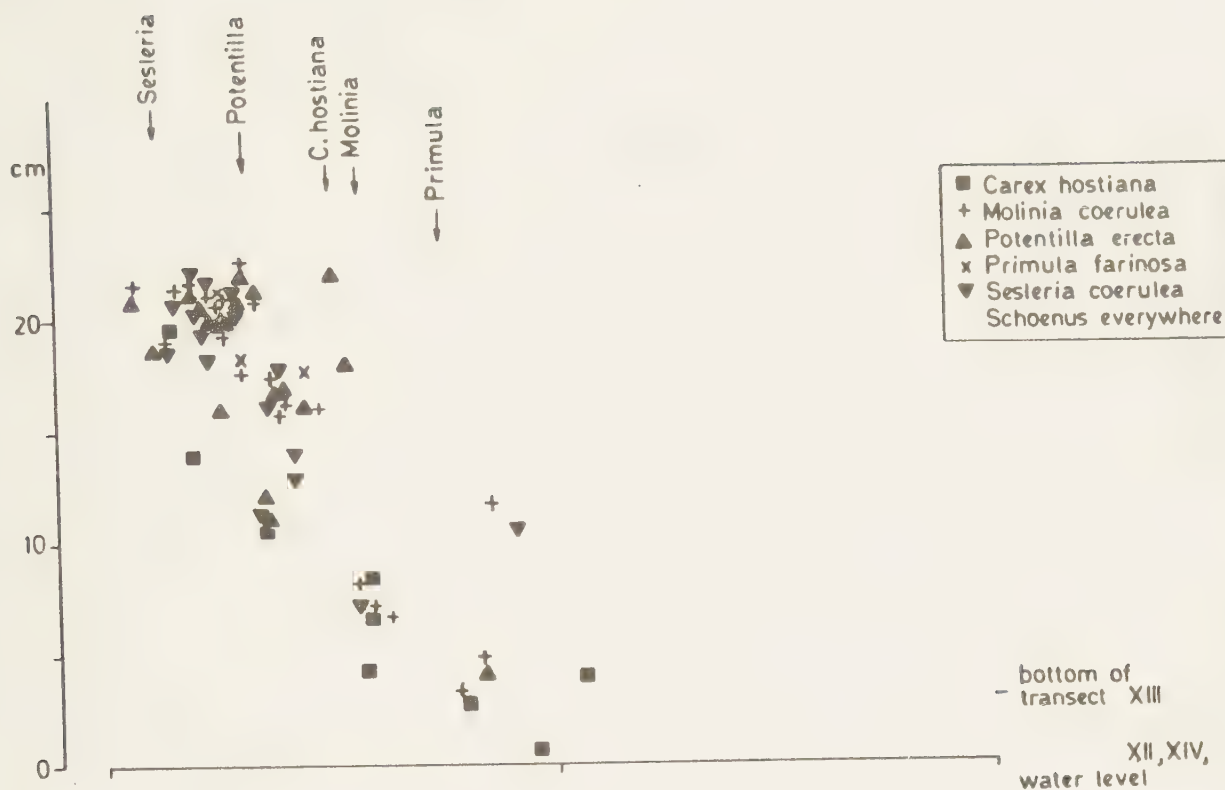


Fig. 12. Same as Fig. 11.

Table 2. Same as Table 1. Öland and Gotland. The species within brackets occurs only on Gotland.

ZONE	1	2	3
HEIGHT LEVEL	< 4	4 - 12	> 12 - 14
BRYOPHYTES	<i>Cratoneuron commutatum</i> * <i>Scorpidium scorpidioides</i> ** <i>Riccardia pinguis</i>	<i>Drepanocladus revolvens</i> * <i>Campylium stellatum</i> ** <i>Cratoneuron commutatum</i> <i>Preissia quadrata</i> <i>Campylium stellatum</i>	<i>Ctenidium molluscum</i> * <i>Fissidens adianthoides</i> ** <i>Ditrichum flexicaule</i> ** <i>Campylium elodes</i>
VASCULAR PLANTS	<i>Utricularia species</i> <i>(Juncus subnodulosus)</i>	<i>Schoenus ferrugineus</i> <i>Eriophorum latifolium</i> <i>Molinia coerulea</i> <i>Carex hostiana</i> <i>Carex dioica</i>	<i>Potentilla erecta</i> <i>Sesleria coerulea</i> <i>Primula farinosa</i> and those from zone 2

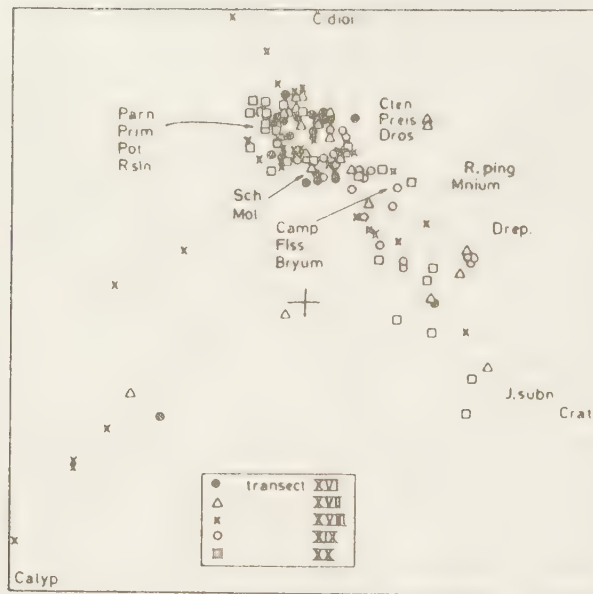


Fig. 13. Plot of species and squares on the plane of axes 1 and 2. Ordination of all transects from Skåne, but squares with presence of *Schoenus nigricans* and *Cephalozia* species are omitted. 149 squares of size 5 x 5 cm., 20 species. Estimated eigenvalues: axis 1, 0.39; axis 2, 0.33.

Species represented in the figure: *Bryum pseudotriquetrum*, *Calypogeia* species, *Campylium stellatum*, *Carex dioica*, *Cratoneuron commutatum*, *Ctenidium molluscum*, *Drepanocladus revolvens*, *Drosera rotundifolia*, *Fissidens adianthoides*, *Juncus subnodulosus*, *Mnium seligeri*, *Molinia coerulea*, *Parnassia palustris*, *Potentilla erecta*, *Preissia quadrata*, *Primula farinosa*, *Riccardia pinguis*, *Riccardia sinuata*, *Schoenus ferrugineus*.

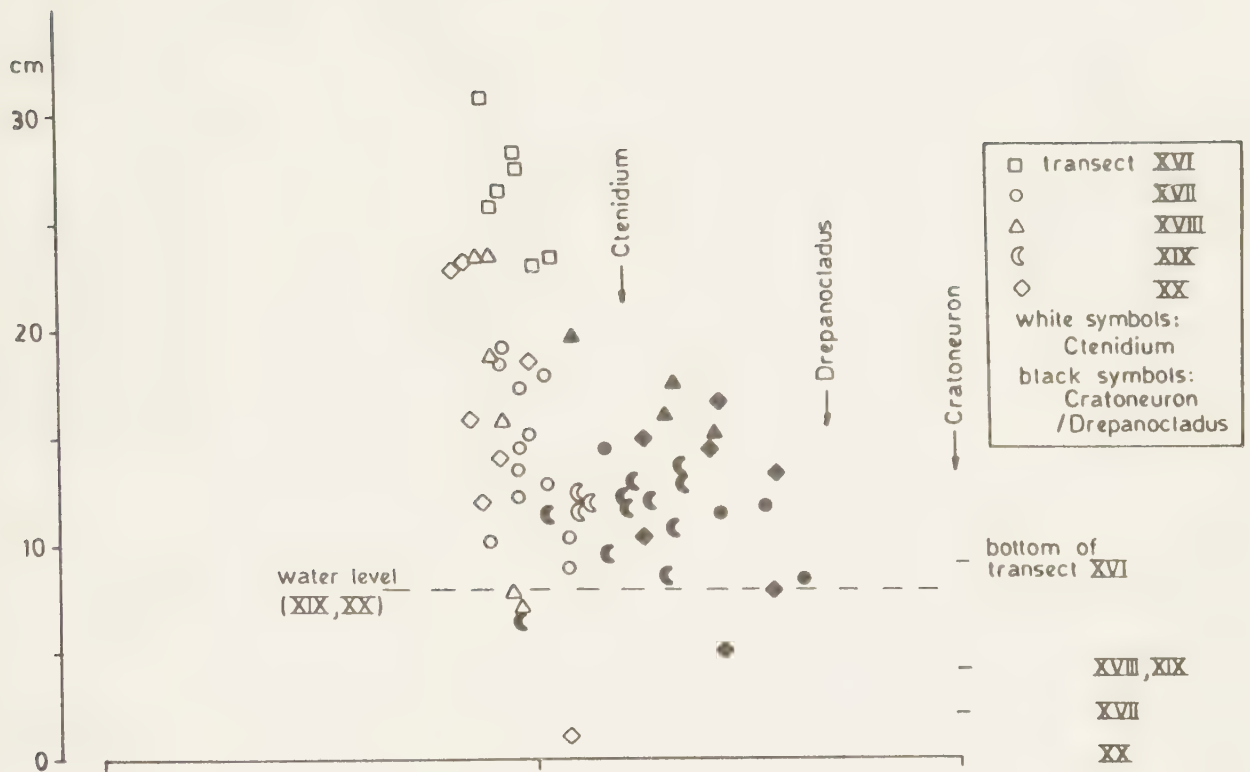


Fig. 14. Scatter diagram of squares with dominance of some bryophytes. X-axis is axis 1 of the same ordination as in Fig. 13.

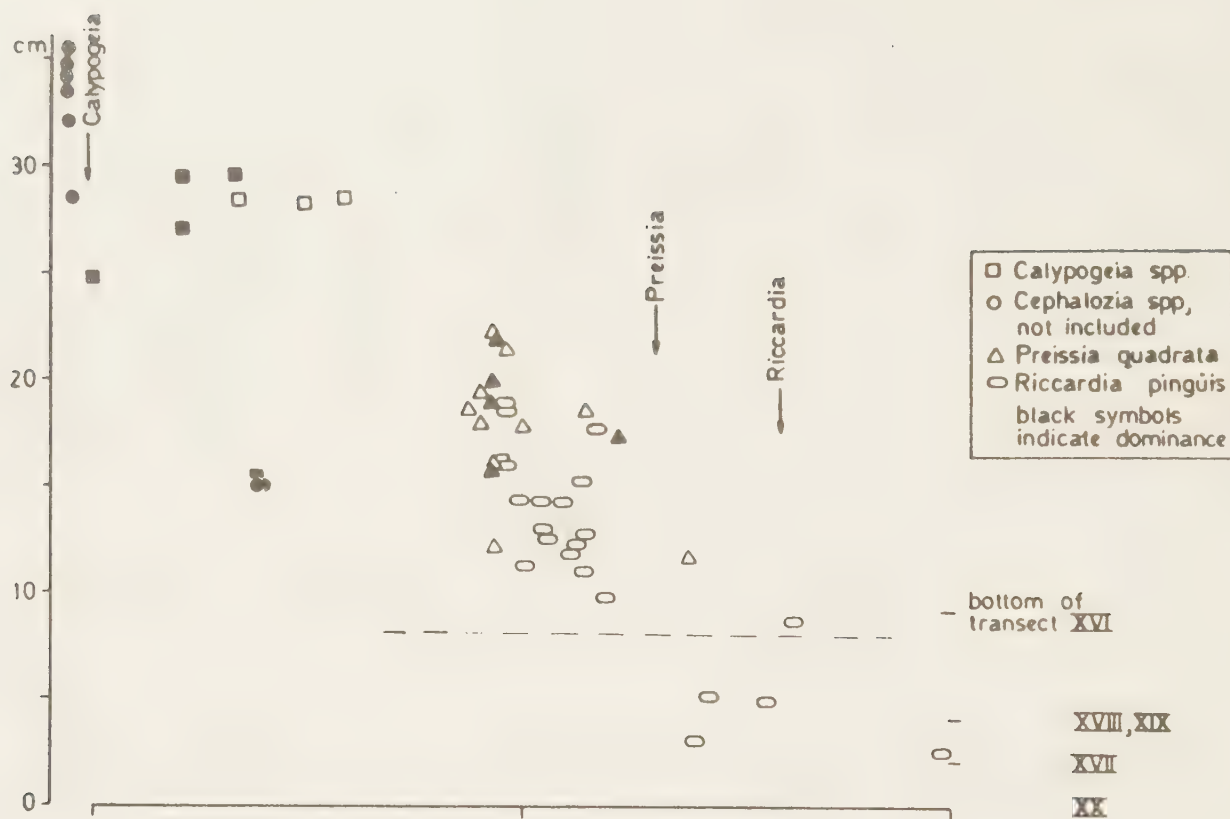


Fig. 15. Scatter diagram of squares with some bryophytes.
Axis and ordination same as in Fig. 14.

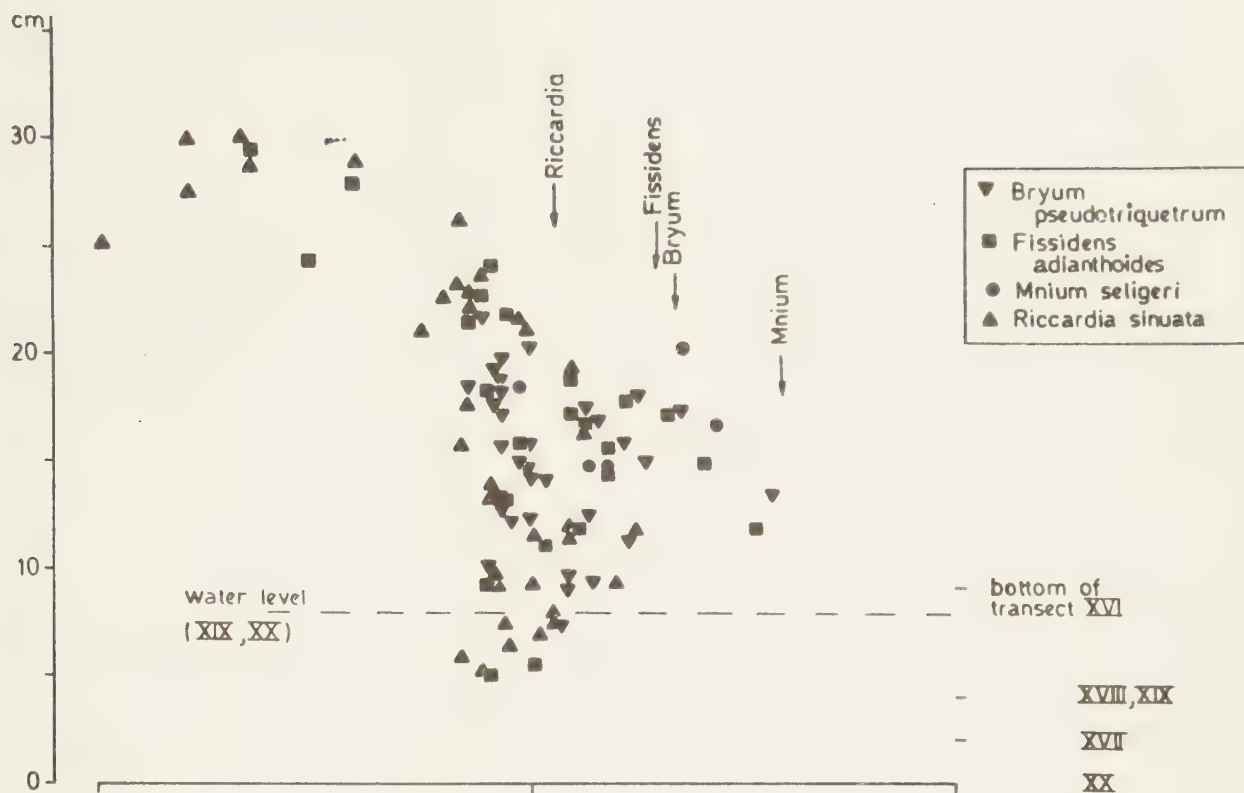


Fig. 16. Same as Fig. 15.



Fig. 17. Scatter diagram of squares with some vascular plants.
Axis and ordination same as in Fig. 14.

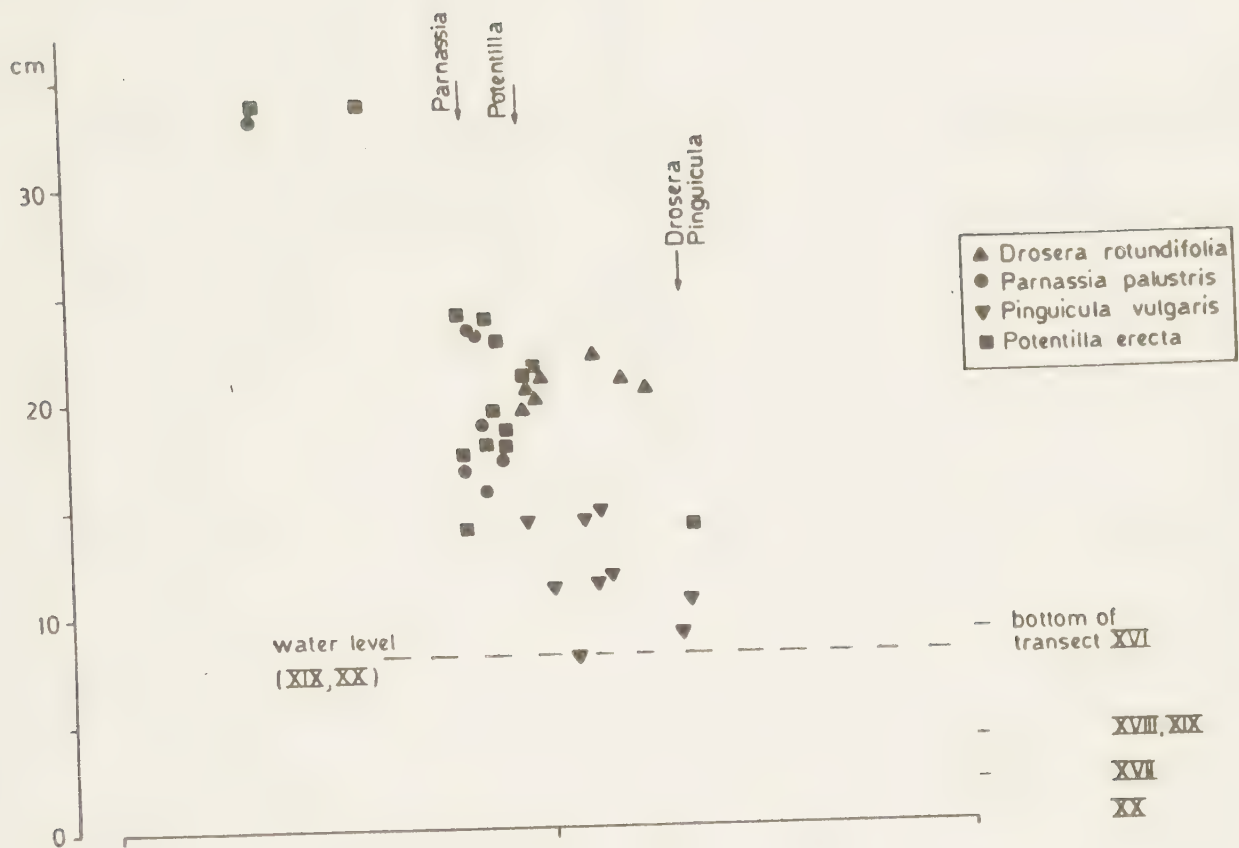


Fig. 18. Same as Fig. 17.

Table 3. Some species with delimited vertical distributions in the transects from Skåne. No sequence of dominance can be given. Height in cm.

Height	<i>Juncus subnodulosus</i> , <i>Riccardia pinguis</i> , <i>Pinguicula vulgaris</i> , <i>Ceratophyllum demersum</i> , <i>Carex flacca</i> , <i>Carex lasiocarpa</i>
<10	
12	, <i>Potamogeton amplifolius</i> , <i>Primula</i>
15	, <i>Potamogeton amplifolius</i> , <i>Potamogeton amplifolius</i>
20	, <i>Potamogeton amplifolius</i> , <i>Potamogeton amplifolius</i>
23	, <i>Potamogeton amplifolius</i> , <i>Potamogeton amplifolius</i>
25	, <i>Potamogeton amplifolius</i> , <i>Potamogeton amplifolius</i>
>25	, <i>Potamogeton amplifolius</i> , <i>Potamogeton amplifolius</i>

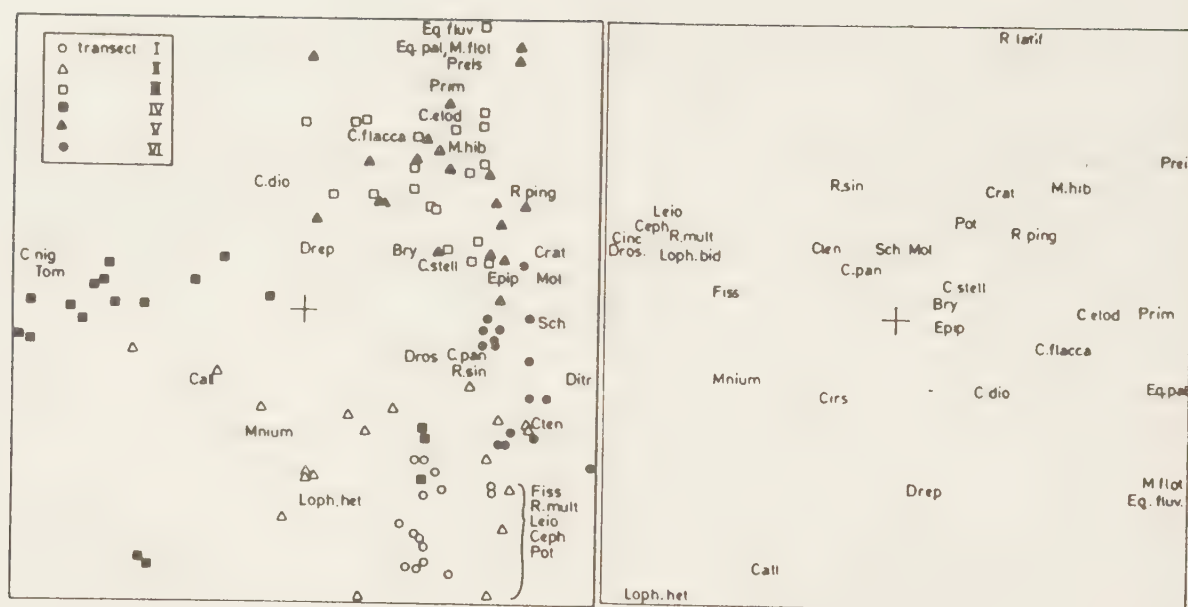


Fig. 19. Plot of species and squares on the plane of axes 1 and 2. Ordination of all transects from Östergötland, 107 squares of size 3 x (2 x 3) cm. and 36 species. Estimated eigenvalues: axis 1, 0.50; axis 2, 0.44.

Species represented in Fig. 19 - 23: *Bryum pseudotriquetrum*, *Calliergonella cuspidata*, *Carex dioica*, *Carex elodes*, *Cephalozia* species, *Carex flacca*, *Cinclidium stygium*, *Cirsium palustre*, *Carex panicea*, *Cratoneuron commutatum*, *Campylium stellatum*, *Ctenidium molluscum*, *Ditrichum flexicaule*, *Drepanocladus revolvens*, *Drosera rotundifolia*, *Epipactis palustris*, *Equisetum fluviatile*, *Equisetum palustre*, *Fissidens adianthoides*, *Leiocolea* species, *Lophocolea bidentata*, *Lophocolea heterophylla*, *Moerckia flotowiana*, *Moerckia hibernica*, *Mnium seligeri*, *Molinia coerulea*, *Potentilla erecta*, *Preissia quadrata*, *Primula farinosa*, *Riccardia latifrons*, *Riccardia multifida*, *Riccardia sinuata*, *Riccardia pinguis*, *Schoenus ferrugineus*, *Tomenthypnum nitens*.

Fig. 20. Plot of species on the plane of axes 1 and 2. Ordination of all transects from Östergötland but with omission of *Tomenthypnum nitens*, *Carex nigra*, and *Ditrichum flexicaule*. 107 squares and 33 species. Estimated eigenvalues: axis 1, 0.45; axis 2, 0.41.

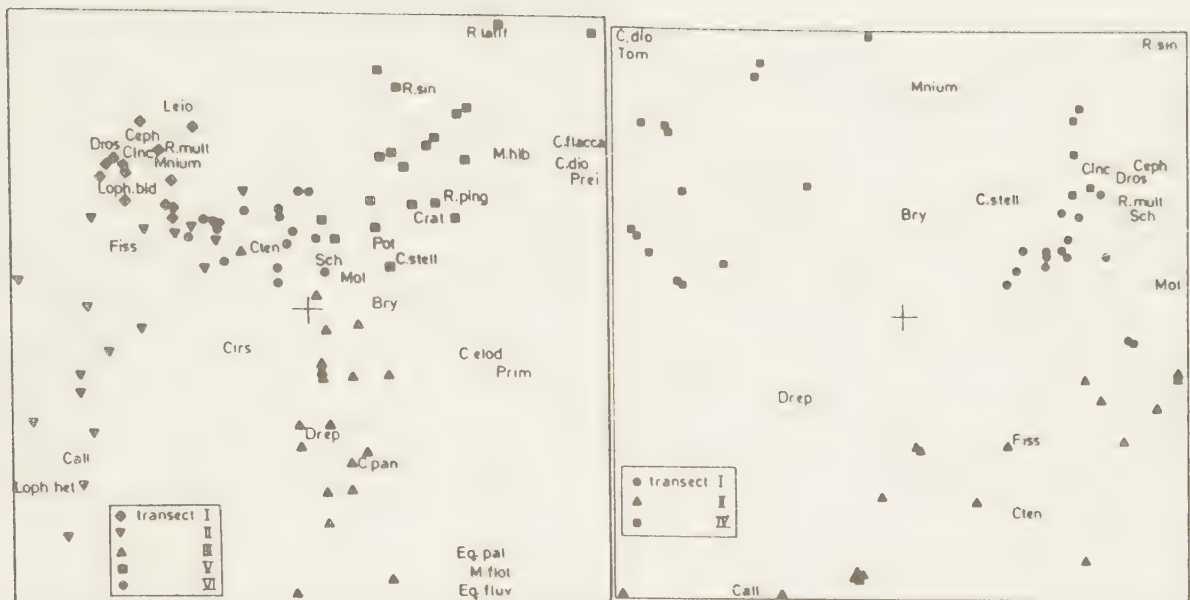


Fig. 21. Plot of species and squares on the plane of axis 1 and 2. Ordination of all transects except IV; 89 squares and 33 species. Estimated eigenvalues: axis 1, 0.49; axis 2, 0.43.

Fig. 22. Plot of species and squares on the plane of axes 1 and 2. Ordination of transects I, II, and IV; 52 squares and 17 species. Estimated eigenvalues: axis 1, 0.50; axis 2, 0.32.

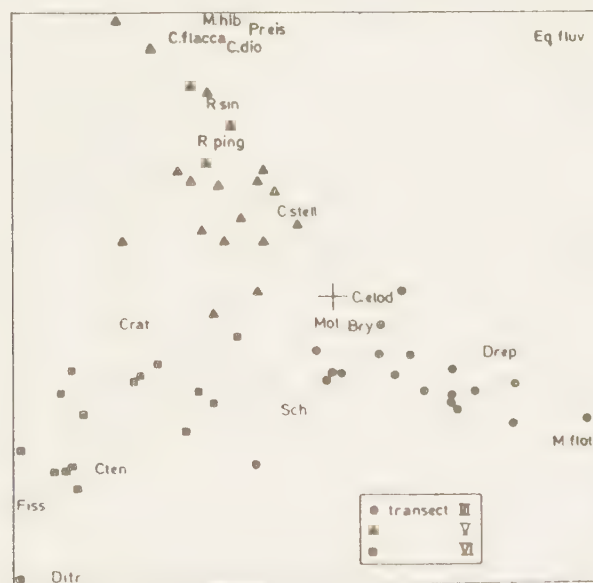


Fig. 23. Plot of species and squares on the plane of axis 1 and 2. Ordination of transects III, V, and VI; 55 squares and 18 species. Estimated eigenvalues; axis 1, 0.48; axis 2, 0.42.

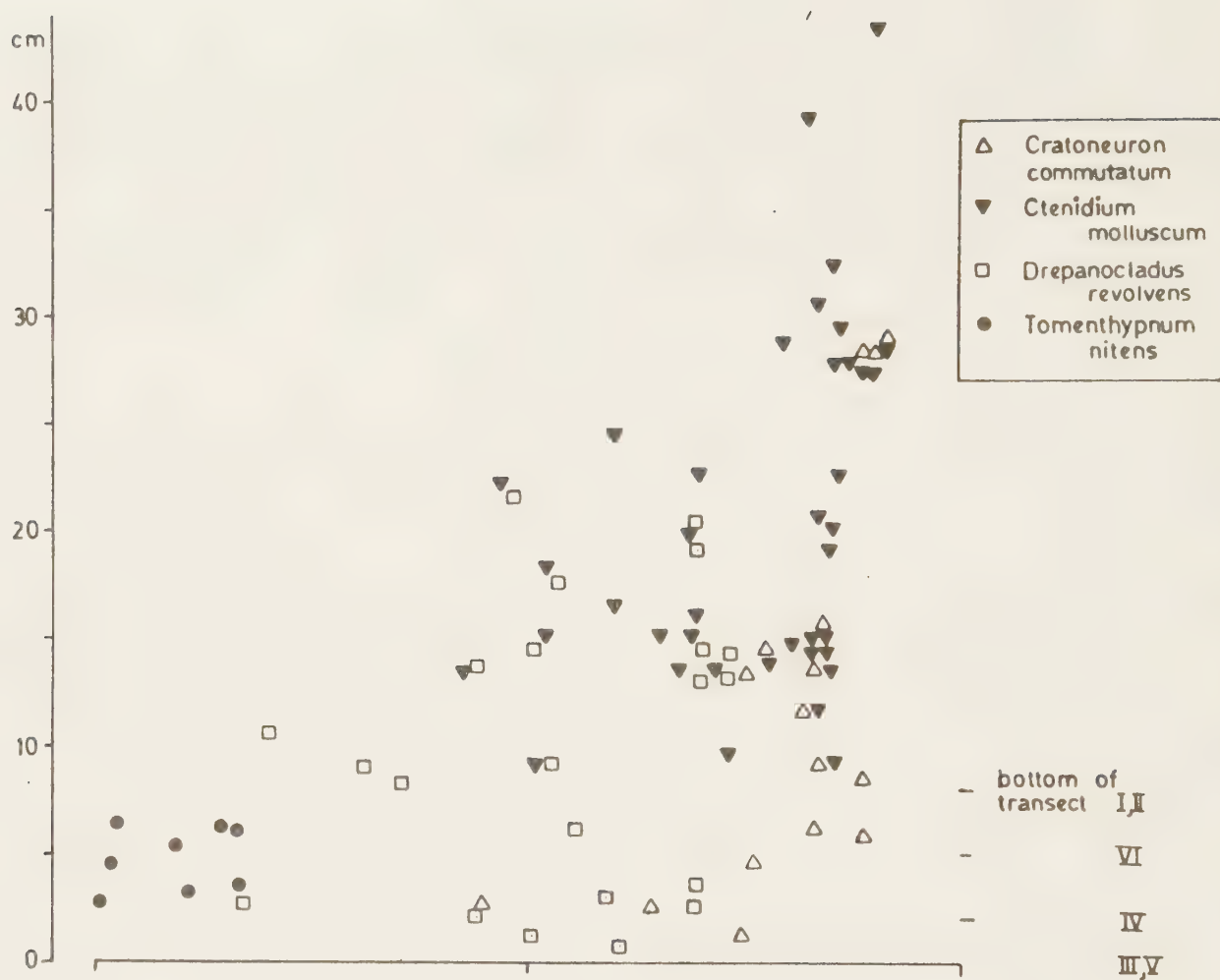


Fig. 24. Scatter diagram of squares with some bryophytes.

X-axis is axis 1 of the same ordination as in Fig. 19.

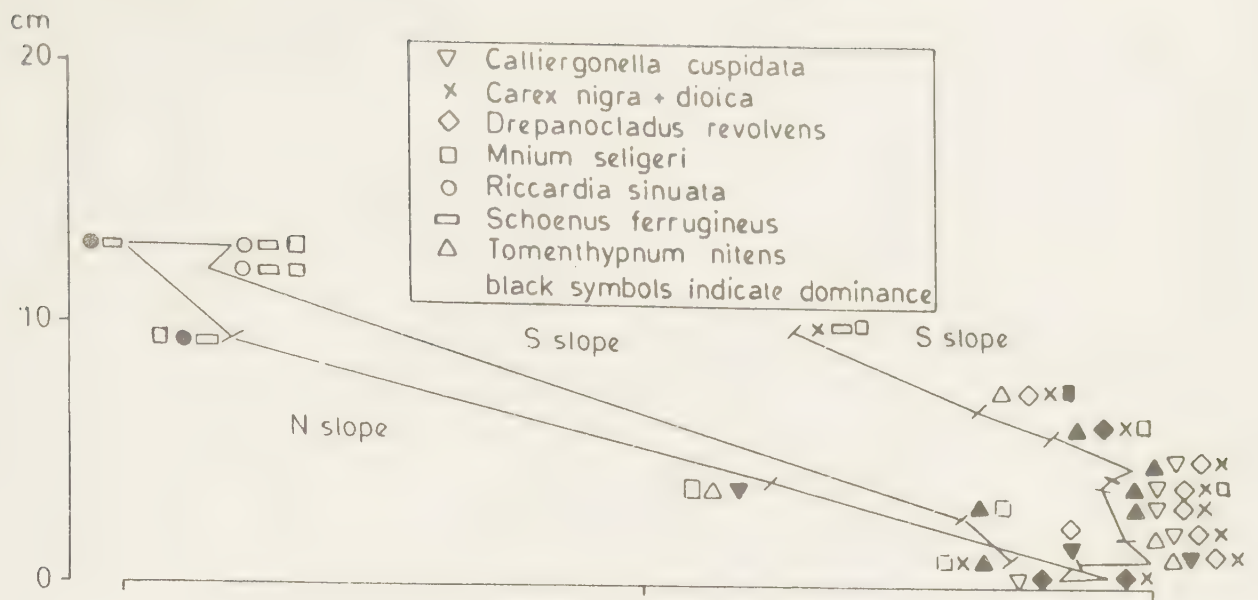


Fig. 25. The presence of certain species in transect IV. The squares are plotted against height levels and according to their scores on axis 1 of the ordination of transect IV; 34 squares and 14 species. A line connects the squares to a picture of the transect and the species are noted according to their occurrences in the squares,

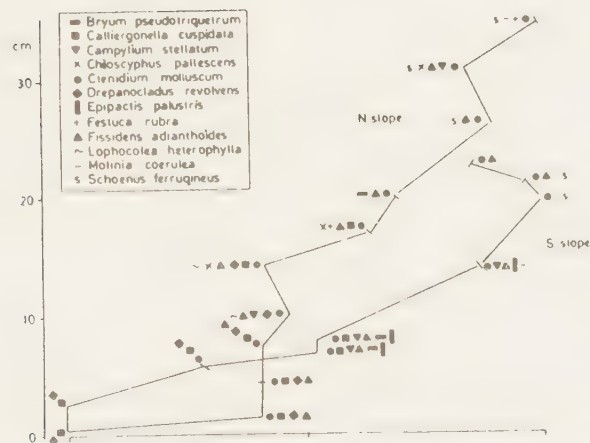


Fig. 26. Same as Fig. 25. Transect II plotted on axis 1 of the same ordination as in Fig. 22.

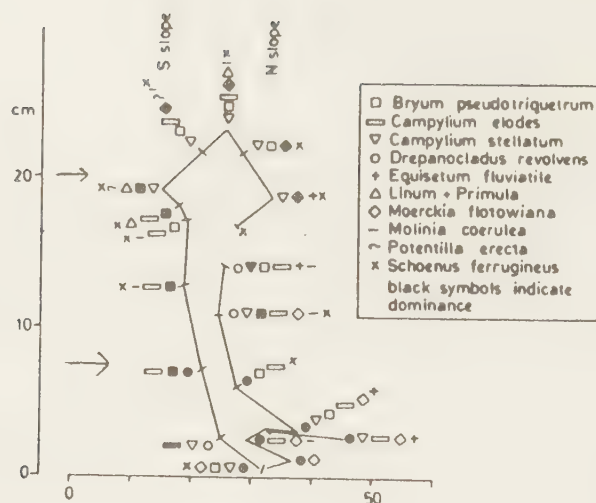


Fig. 27. Same as Fig. 25. Transect III plotted on axis 2 obtained by ordination of the transects III and V; 39 squares and 17 species. The arrows indicate pH levels, cf. Fig. 29.

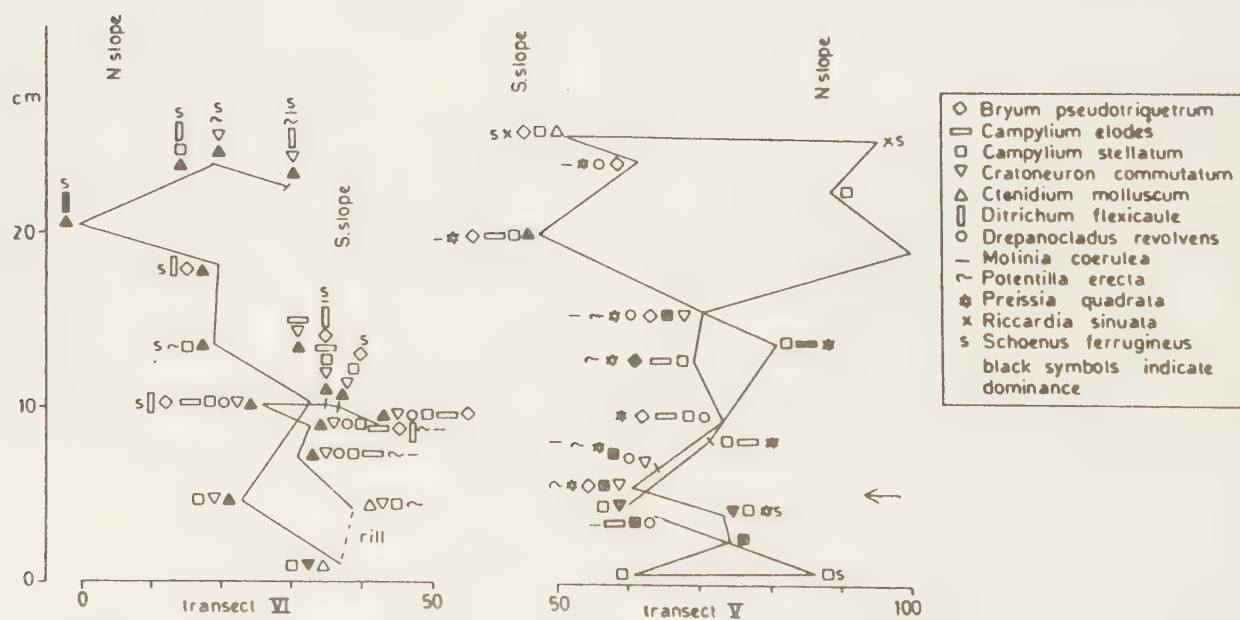


Fig. 28. Same as Fig. 25. Transects V (right) and VI (left) plotted on axis 2 of the same ordination as in Fig. 23. The arrow indicates pH levels, cf. Fig. 29.

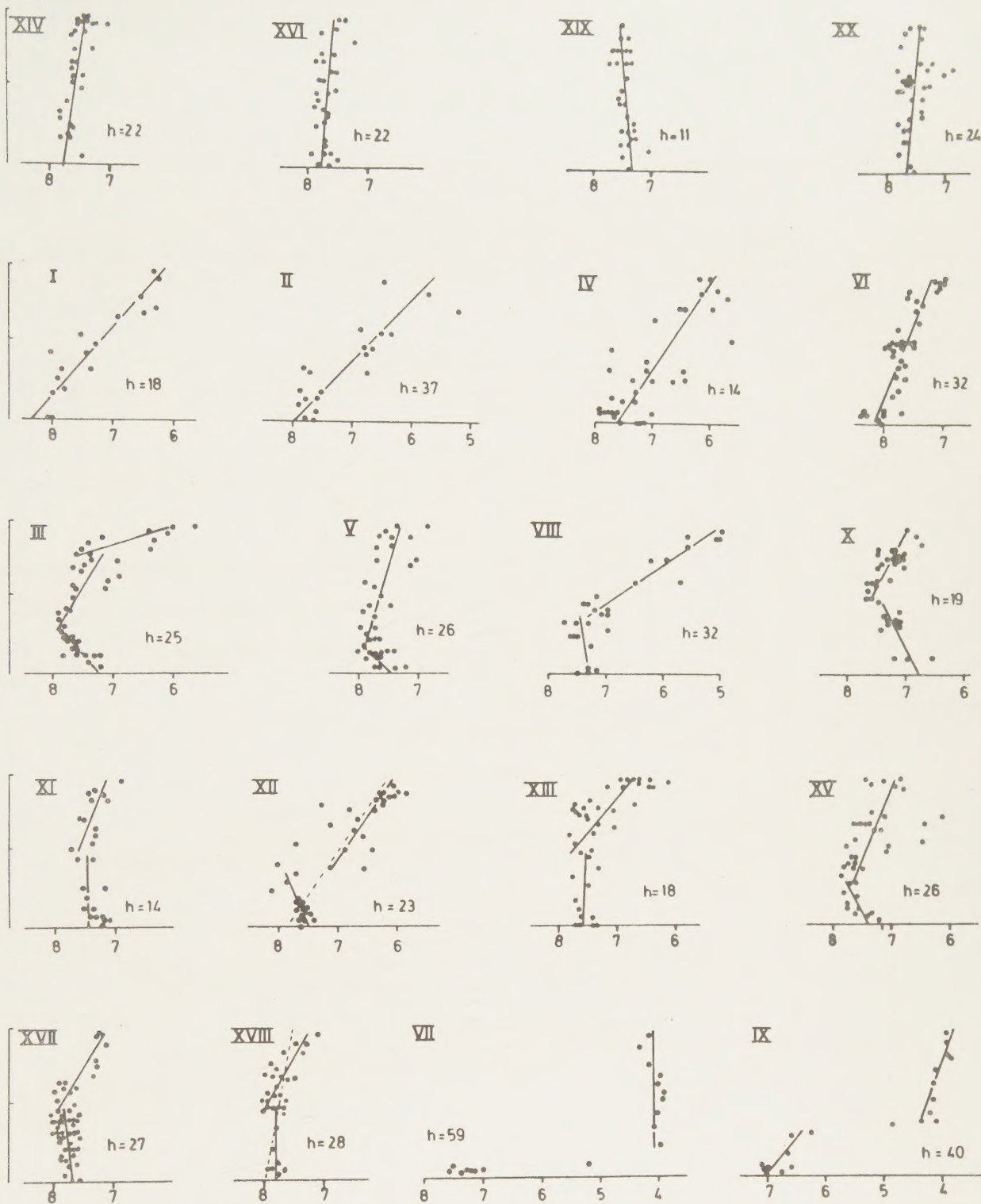


Fig. 29. Relationship between pH (y, horizontally) and height index (x, vertically) of each transect. Total height of the transect (h) and regression line of the regression of y on x (cf. Table 4) are given. Transects I - VI are studied in Östergötland, VII - X in Uppland, XI on Gotland, XII - XV on Öland, and XVI - XX in Scania.

Table 4. Standard deviations of y (pH) and the probability of departure from zero of the regression coefficient, b, tested by t-test if $N \leq 30$ or standard error if $N > 30$. $P = 0.05 *$, $0.01 **$, $0.001 ***$. The most important bryophytes with regard to change in dominants and/or species composition are given, w is the whole transect, a and b the lower and higher part respectively. Species given only with names of genus: *Bryum pseudotriquetrum*, *Calliergonella cuspidata*, *Calypogeia fissa* and *mülleriana*, *Campylium stellatum*, *Cratoneuron commutatum*, *Ctenidium molluscum*, *Ditrichum flexicaule*, *Drepanocladus revolvans*, *Preissia quadrata*, *Scorpidium scorpidioides*, *Tomenthyprum nitens*.

Transect no. and part	N	SD	b $\neq$ 0	Bryophytes
I	16	.28		Mixture of <i>Drepanocladus</i> , <i>Campylium</i> , <i>Ctenidium</i> , <i>Bryum</i>
II	20	.40	***	<i>Ctenidium</i> , <i>Fissidens</i> everywhere, <i>Drepanocladus</i> , <i>Calliergonella</i> in lower part
III a	16	.15	**	<i>Drepanocladus</i> dominant
b	16	.26	**	<i>Bryum</i> dominant
c	11	.45	**	<i>Moerckia flotowiana</i> dominant
IV	35	.42	***	<i>Calliergonella</i> , <i>Tomenthyprum</i> in lower part, <i>Campylium stellatum</i> in higher part
V a	16	.20		<i>Cratoneuron</i> dominant, <i>Campylium</i> , <i>Ctenidium</i>
b	24	.23	***	<i>Preissia</i> , <i>Ctenidium</i> dominants, <i>Campylium</i>
VI	40	.19	***	<i>Ctenidium</i> dominant, <i>Cratoneuron</i>
VII b	10	.21		<i>Campylium</i> not present, <i>Sphagnum fuscum</i> dominant, VII a <i>Campylium</i> , <i>Sphagnum fuscum</i> dominants
VIII a	12	.21		<i>Scorpidium</i> , <i>Campylium</i> dominants
b	16	.32		<i>Sphagnum rubellum</i> present, dominant in higher part, <i>Campylium</i> , <i>Tomenthyprum</i> in lower part
IX a	9	.20	*	<i>Drepanocladus</i> , <i>Campylium</i> dominants
b	11	.19	**	<i>Sphagnum warnstorffii</i> , <i>Sphagnum rubellum</i> , <i>Sphagnum fuscum</i> dominants
X a	13	.18	*	<i>Scorpidium</i> , <i>Drepanocladus</i> dominants
b	25	.18	***	<i>Campylium</i> dominant
XI a	18	.24		<i>Cratoneuron</i> dominant
b	12	.17	*	<i>Campylium</i> , <i>Drepanocladus</i> dominants
XII w	42	.36	***	
a	19	.12	**	<i>Scorpidium</i> , <i>Drepanocladus</i> dominants
b	23	.42	***	no dominants
XIII a	14	.14		<i>Campylium stellatum</i> dominant, <i>Drepanocladus</i> , <i>Scorpidium</i>
b	29	.35	***	<i>Campylium stellatum</i> , <i>Campylium elodes</i> , <i>Ditrichum</i> dominants
XIV	30	.14	***	<i>Scorpidium</i> , <i>Campylium stellatum</i> , <i>Campylium elodes</i> dominants at different levels
XV a	11	.16		<i>Cratoneuron</i> dominant
b	31	.15	***	<i>Ctenidium</i> , <i>Campylium elodes</i> dominants
XVI	32	.14	***	<i>Ctenidium</i> present everywhere, <i>Campylium</i> , <i>Ctenidium</i> , <i>Cephalozia</i> dominants at different levels
XVII a	39	.12		<i>Drepanocladus</i> , <i>Cratoneuron</i> , <i>Ctenidium</i> dominants
b	16	.18	***	<i>Preissia</i> , <i>Ctenidium</i> dominants in lower part, no dominants in higher part
XIIX w	36	.18	***	mixed dominance of <i>Drepanocladus</i> , <i>Campylium</i> , <i>Ctenidium</i> at all levels
a	15	.11		
b	21	.15	***	<i>Calypogeia</i> , <i>Riccardia sinuata</i> dominants on the top
XIX	30	.11	**	Mixed presence and dominance of <i>Drepanocladus</i> , <i>Campylium</i> , <i>Ctenidium</i>
XX	35	.22		Mixed presence and dominance of <i>Drepanocladus</i> , <i>Campylium</i> , <i>Ctenidium</i>

